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Three new species of cave *Troglopedetes* (Collembola, Paronellidae, Troglopedetinae) from Thailand, with a key to the Thai species

Katthaleeya Surakhamhaeng[1], Louis Deharveng[2], Sopark Jantarit[3]

1 *Division of Biological Science, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla, 90110, Thailand* **2** *Institut de Systématique, Evolution, Biodiversité (ISYEB) - UMR 7205 CNRS, MNHN, UPMC, EPHE, Museum national d'Histoire naturelle, Sorbonne Université, 45 rue Buffon, CP50, F-75005 Paris, France* **3** *Excellence Center for Biodiversity of Peninsular Thailand, Faculty of Science, Prince of Songkla University, Hat Yai, Songkhla, 90110, Thailand*

Corresponding author: Sopark Jantarit (fugthong_dajj@yahoo.com)

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Abstract

Thailand is today the richest country for the genus *Troglopedetes* Joseph, 1872, with 17 species described from the country. In this study three troglomorphic new species are described from caves in the western region. They are *T. spectabilis* **sp. nov.** and *T. rungsimae* **sp. nov.** from Kanchanaburi province and *T. takensis* **sp. nov.**, from Tak province. The three new species share elongated antennae and have the same number of central mac on Th. III and Abd. IV. However, they differ from one another by the combination of: presence of eyes, antennal length, claw morphology, central head macrochaetotaxy and internal row of dental spines. *Troglopedetes spectabilis* **sp. nov.** is remarkably different from its congeners by its extreme long appendages, especially the antennae (ratio antenna: head = 5.5). In the second part of the paper the arrangment of antennal chaetotaxy and the diversity of its phaneres is analyzed in the three new species, homologized and compared with those of two other species described from Thailand (*T. meridionalis* and *T. kae*). A total of 22 types of chaetae have now been recognized among the species. A new type of S-chaetae for the genus was discovered in this study. There are 5 types of ordinary chaetae, 15 types of S-chaetae, the subapical organite of Ant. IV and scales. A total of 1,107 to 2,183 antennal chaetae on each side were observed, which includes 308–485 S-chaetae, 687–1,402 ordinary chaetae, 72–295 scales and a subapical organite.

Keywords

Antennal phaneres, cave, chaetotaxy, Southeast Asia, subterranean habitat, troglomorphy

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Introduction

The genus *Troglopedetes* Joseph, 1872 is widespread in Thailand in both edaphic and subterranean environments, particularly in the western and northern regions of the country (Deharveng 1987; Jantarit et al. 2020). Two species were recently described from southern Thailand (*T. meridionalis* Jantarit, Surakhamhaeng & Deharveng, 2020 and *T. kae* Jantarit, Surakhamhaeng & Deharveng, 2020), and these were the first records of the genus from the south of the Kra Isthmus, a major zoogeographical boundary in this region (Jantarit et al. 2020). Today Thailand is the richest country for the genus *Troglopedetes*, of which 14 species have been described, all troglobitic. There are 8 described species from northern Thailand (*T. centralis* Deharveng & Gers, 1993, *T. fredstonei* Deharveng, 1988, *T. leclerci* Deharveng, 1990, *T. longicornis* Deharveng & Gers, 1993, *T. maffrei* Deharveng & Gers, 1993, *T. maungonensis* Deharveng & Gers, 1993, *T. microps* Deharveng & Gers, 1993 and *T. multispinosus* Deharveng & Gers, 1993), 4 species from western Thailand (*T. calvus* Deharveng & Gers, 1993, *T. convergens* Deharveng & Gers, 1993, *T. dispersus* Deharveng & Gers, 1993 and *T. paucisetosus* Deharveng & Gers, 1993) and 2 species from southern Thailand (*T. kae* and *T. meridionalis*) (Deharveng 1988a, 1990; Deharveng and Gers 1993; Jantarit et al. 2016, 2020). They all have a limited distribution range and many of them are restricted to the cave where they were described. From our study and intensive survey, more than 200 caves throughout the country, *Troglopedetes* spp. were present in 46 caves, and most of them are undescribed (Fig. 1).

Troglomorphic features in Collembola mostly comprise: large body size, elongated appendages (antennae, legs and furca), elongated and slender claw complex, pointed tenent hair, multiplication of antennal chaetae, blindness and depigmentation (Christiansen 2012; Deharveng and Bedos 2018; Lukić et al. 2018; Jantarit et al. 2019; Lukić 2019). The *Troglopedetes* species is so far described from Thailand exhibit various degrees of troglomorphy. Most of them are blind (only *T. leclerci* and *T. microps* have eyes), some are pigmented with orange dots, while others are white. They have various body sizes and antennal lengths, claw and furca morphologies. Among the 14 described species from Thailand, only *T. multispinosus* and *T. longicornis* display marked troglomorphic characters by having the most elongated antennae (ratio of antennae: body = 0.9 and 0.8 respectively), larger body size (1.8–2.2 mm), slender claw complex and pointed tenent hairs. The other described species have shorter antennae (ratio of antennae: body = 0.4–0.6), shorter body length (0.7–1.7 mm) and different claw complex morphology (Deharveng 1988a, 1990; Deharveng and Gers 1993; Jantarit et al. 2020).

During our sampling campaigns in limestone caves in Thailand, several *Troglopedetes* species were collected. Three of them, which were found in caves in the western region (Tak and Kanchanaburi provinces), are described in this study. One of them exhibits strikingly long antennae, not seen in any other species of the genus (ratio of antennae: head > 3 times; antennae: body ≥ 1).

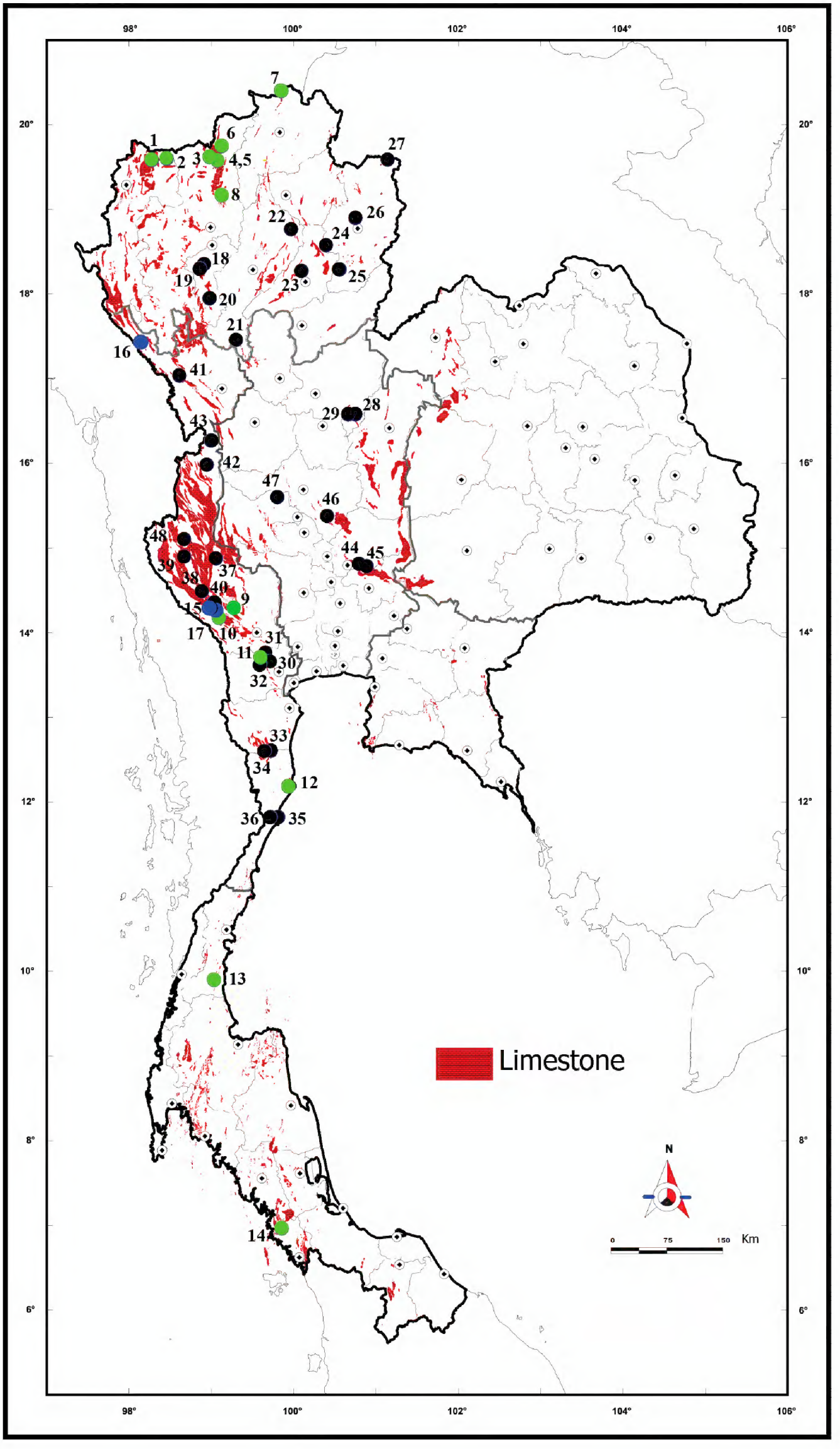
We have already described a high diversity of phaneres on antennae of two species of *Troglopedetes* (Jantarit et al. 2020), expecting that the antennal chaetotaxy could bring valuable information at the taxonomic level, as they do in Poduromorpha (Deharveng 1981), and could be used as important tools once patterns in other Entomobryoidea are better understood (Jantarit et al. 2020). In the second part of this paper, we complete the data obtained so far by analysing, homologising and comparing the antennal chaetotaxy of the three new species with that of *T. meridionalis* and *T. kae* from Thailand, which have been previously described in this respect. A complete catalogue of all antennal chaetae is also provided. One of the three new species has extremely elongated antennae and is of special interest, as the increase in the number of sensory chaetae on the antennae of modified cave species has been considered in the literature as a troglomorphic trend in the genus *Pseudosinella* Schäffer, 1897 (Deharveng 1988b). The third part of the paper is a key to the species of the genus in Thailand.

Materials and methods

The specimens of the three new species were collected in the dark zone of caves in Tak and Kanchanaburi Province (Fig. 1). Collembola were detected by eye and then collected by aspirator. They were stored in 95% ethanol. For microscopical observation, they were mounted on slides in Marc Andre II medium after clearing in lactic acid. Morphological characters were examined under a light microscope using Leica DMLB and Leica DM1000 LED microscope with phase-contrast. Drawings were made using a drawing tube, and figures were improved with Adobe Photoshop and Illustrator CC/PC (Adobe Inc.).

Abbreviations

Ant.	antennal segment;
Abd.	abdominal segment;
AIIIO	apical organ of Ant. III;
Th.	thoracic segment;
mac	macrochaetae;
mes	mesochaetae;
mic	microchaeta;
psp	pseudopore;
Tita	tibiotarsus;
tric	trichobothria;
ms	S-microchaeta(e);
s or sens	S-chaeta(e);
VT	ventral tube;
NHM-PSU	Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Songkhla, Thailand.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45
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47
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Figure 1. Distribution of *Troglopedetes* in Thailand (green circles) with limestone terrains (red colour) of the country **1** *T. maffrei* Deharveng & Gers, 1993 **2** *T. longicornis* Deharveng & Gers, 1993 **3** *T. centralis* Deharveng & Gers, 1993 **4** *T. fredstonei* Deharveng, 1988 **5** *T. leclerci* Deharveng, 1990 **6** *T. microps* Deharveng & Gers, 1993 **7** *T. multispinosus* Deharveng & Gers, 1993 **8** *T. maungonensis* Deharveng & Gers, 1993 **9** *T. calvus* Deharveng & Gers, 1993 **10** *T. dispersus* Deharveng & Gers, 1993 **11** *T. convergens* Deharveng & Gers, 1993 **12** *T. paucisetosus* Deharveng & Gers, 1993 **13** *T. meridionalis* Jantarit, Surakhamhaeng & Deharveng, 2020 **14** *T. kae* Jantarit, Surakhamhaeng & Deharveng, 2020 **15** *T. spectabilis* sp. nov. **16** *T. takensis* sp. nov. **17** *T. rungsimae* sp. nov. (blue circles) and undescribed species of *Troglopedetes* found in Thailand (black circles). Regional boundary indicated by grey line; province capitals as small dark dots; scale 1:250,000.

Conventions for describing pseudopore and chaetotaxic patterns

Pseudopore arrangement follows Deharveng et al. (2018) and Jantarit et al. (2020). Types of phaneres follows Jantarit et al. (2020). Formula of tergite pseudopores is given by half-tergite from Th. II to Abd. IV (Jantarit et al. 2013). Formula for labium basis chaetae follows the system of Gisin (1967), with upper-case letters for ciliated and lower-case letters for smooth chaetae. Labial chaetotaxy follows Fjellberg (1999). Dorsal chaetotaxy and chaetal areas of the head follow Deharveng and Gers (1993), Jordana and Baquero (2005) and Mitra (1993). Dorsal macrochaetotaxy description combines notation of individual chaetae derived from Szeptycki (1979) with chaetal group notation (rationale in Soto-Adames et al. 2014 and Jantarit et al. 2020). Formula of dorsal macrochaetae and trichobothria are given by half-tergite from head to Abd. IV; for S-chaetae, by half-tergite from head to Abd. V. S-chaetae terminology of tergites follows Zhang and Deharveng (2014) and Jantarit et al. (2020).

Taxonomy

Family Paronellidae Börner, 1906
Subfamily Troglopedetinae Börner, 1913
Genus *Troglopedetes* Joseph, 1872

1. *Troglopedetes spectabilis* sp. nov.

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Figs 2–7, 16A

Type locality. Thailand, Kanchanaburi province, Sai Yok district, Tham (cave) Morakhot (14°11'02.7"N, 99°01'32.8"E, 426 m a.s.l.).

Type material. ***Holotype*:** female on slide, Kanchanaburi province: Sai Yok district, Tham (cave) Morakhot, 14°11'02.7"N, 99°01'32.8"E, 426 m a.s.l., 28 February 2019, S. Jantarit, A. Nilsai and K. Jantapaso leg., dark zone of cave, by aspirator (sample # THA_SJ_KRI12). ***Paratypes*:** 5 paratypes on slides (all subadults), same locality and date as the holotype.

Table 1. *Troglopedetes spectabilis* sp. nov., measurements in µm (from holotype).

Head		Tergites		Appendages	
Ant. I	374	Th. II	230	Man	560
Ant. II	667	Th. III	180	Dens	736
Ant. III	720	Abd. I	100	Mucro	53
Ant. IVa	595	Abd. II	120	Furca	1,349
Ant. IVb	424	Abd. III	135	Claw I	64
Ant.	2,780	Abd. IV	550	Claw II	64
Head	500	Abd. V	90	Claw III	65
		Abd. VI	70		
		Body	1,475		

Holotype and 5 paratypes deposited in NHM-PSU, measurements of holotype in Table 1.

Description. ***Habitus.*** Highly troglomorphic, slender, with elongate legs, furca and antennae (Figs 2A, 16A). Length: 1.7–2.1 mm (n = 6) (body 1.5–1.7 mm, head 0.4–0.5 mm). Fourth abdominal segment 4–6 times (n = 6, female and 5 subadults) longer than the third one along the dorsal axis. Furca well developed, about 1.1–1.2 (n = 3) times shorter than body length. Body colour white, with spots of orange pigment. Eyes absent, no ocular patch.

Chaetal types. Four types of chaetae on somites, appendages (except antennae) and mouthparts: scales, present on antennal segment I and II, head, body and ventral side of the furca, absent on legs and ventral tube; ordinary chaetae on all body parts; S-chaetae and trichobothria on tergites; hairs devoid of sockets on outer maxillary lobe. Chaetal types on antennae are much more diverse and described separately further.

Pseudopores (Figs 2E, 3A–D, 4G, 5B, 6B, 6D). Pseudopores present as round flat disks larger than mac sockets, on antennae, head and tergites. Head pseudopore sometimes present asymmetrically on one side only (Fig. 2E). Dorsal pseudopore formula: 1/1, 1/1, 1, 1, 1+4 (Figs 2E, 3A–D). On antenna, 2 psp detected ventro-distally on Ant. I, 3 ventro-distally on Ant. II and 1 ventro-distally on Ant. III (Figs 5B, 6B, 6D). On head, 1 psp close to antennal basis (Fig. 2E). On legs, psp present externally on coxae (2 for legs I and II and 2–(3) for leg III). On manubrium, 2 psp on the dorso-distal plaque (Fig. 4G); on each dens, 4 psp dorso-basally near the internal spine row (Fig. 4G).

Mouthparts. Clypeus with 11 mac, symmetrically arranged: 9 ciliated posteriorly and 2 smooth anteriorly (Fig. 2F). Labral formula 4/5,5,4 (Fig. 2I; prelabral chaetae short, bent and ciliated, labral chaetae thinner, longer, smooth and acuminate, those of the distal row slightly larger and longer than those of the median row; its anterior line not concave in V or U-shape, contrary to *T. kae* (Jantarit et al. 2020). Ventro-distal complex of labrum well differentiated, asymmetrical, with 2 distal combs (a larger one with 8–12 teeth on the left side, a smaller one with 15–19 minute teeth on the right side) and an axial pair of sinuous tubules (Fig. 2C). Distal part of labrum not adorned with spines dorso-distally. Labial palp similar to that described by Fjellberg (1999) for *Troglopedetes* sp., with strong papillate chaetae. Number of guards for each major

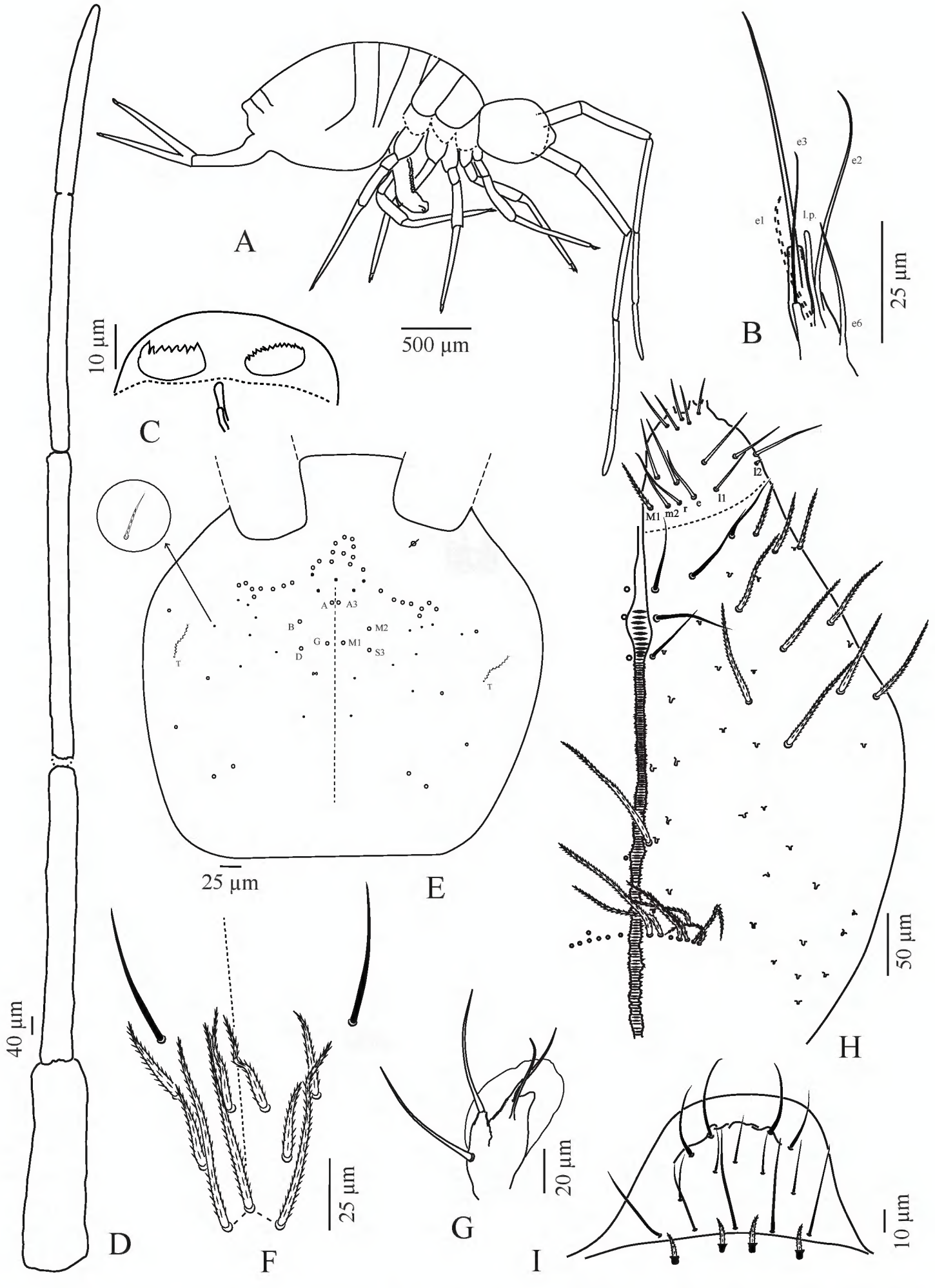

Figure 2. *Troglopedetes spectabilis* sp. nov. **A** habitus **B** papilla E of labial palp **C** ventro-distal complex of labrum **D** antenna E head chaetotaxy (left = A to G mac nomenclature; right = AMS nomenclature) **F** Clypeus **G** outer maxillary lobe **H** labial basis and ventral chaetotaxy of head, right side **I** labrum.

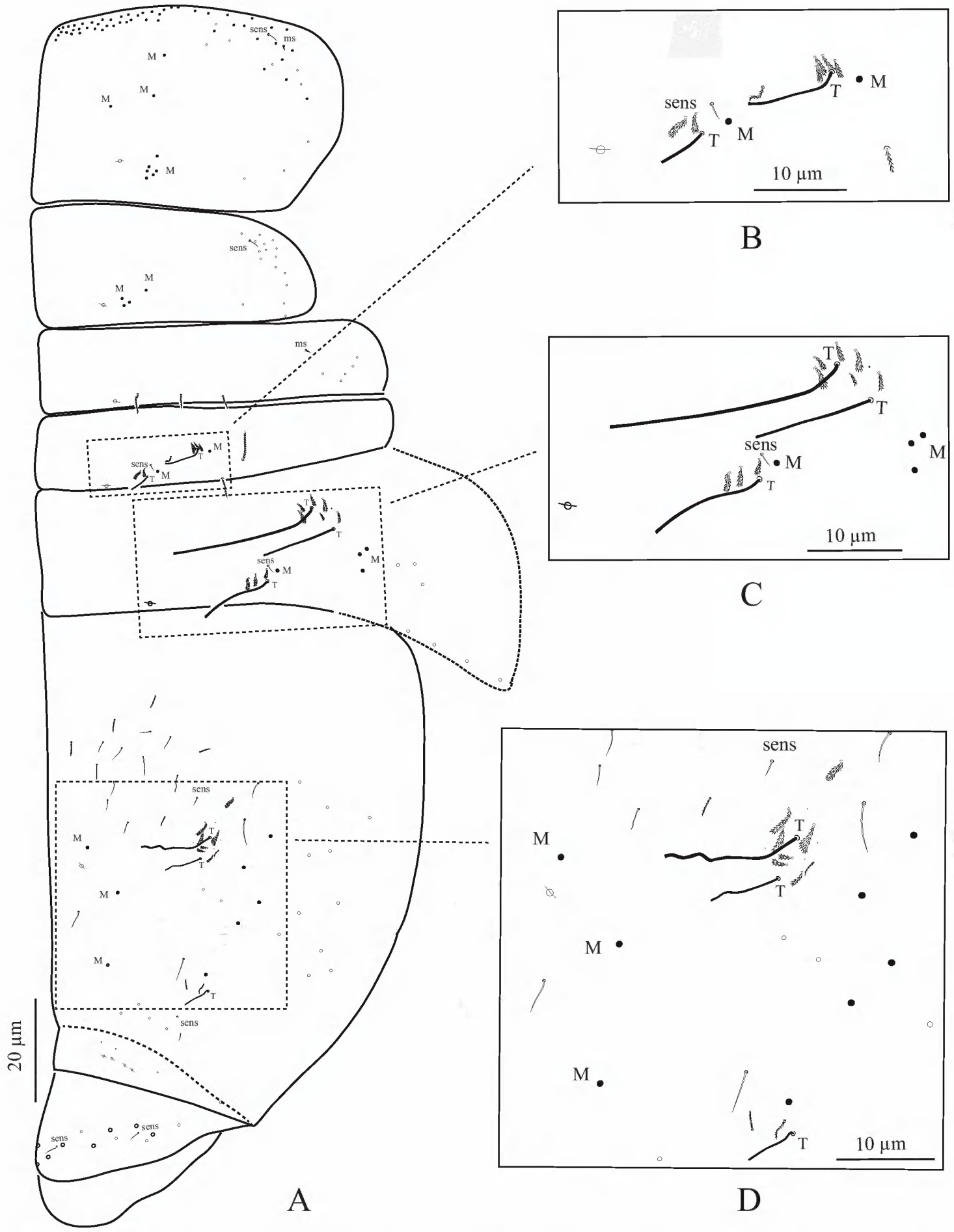

Figure 3. *Troglopedetes spectabilis* sp. nov., continued **A** chaetotaxy of tergites **B** trichobothrial complexes of Abd. II **C** trichobothrial complexes of Abd. III **D** trichobothrial complex of Abd. IV.

papillate chaetae: A (0), B (5), C (0), D (4) and E (4); lateral process subcylindrical, reaching above the apex of papilla E (Fig. 2B); 5 proximal chaetae. Chaetae of labial basis as M1m2rel1l2, with M1 ciliated, m2, e and l1 subequal and smooth, r shorter than others and smooth, l2 short, smooth and acuminate (Fig. 2H). Outer maxillary

lobe with 1 papillate chaeta, 1 basal chaeta and 2 sublobal hairs, shorter than the others (Fig. 2G). Maxillary head with a 3-toothed claw, several stout shortly ciliated lamellae not observed in detail and 2 thin elongate structures (1 dorsally and 1 ventrally), like in *T. kae* (Jantarit et al. 2020). Mandible head strong, asymmetrical (left side with 4 teeth, right side with 5); molar plate with 3 strong pointed basal teeth, and other 2–3 inner distal teeth, identical in both mandibles.

Antennae (Figs 2A, 2D, 5–7). Antennae extremely elongated (2,175–2,780 μm, n = 6), 1.45–1.64 times longer than body+head length (n = 3), 5.5 times (n = 4) longer than the cephalic diagonal. Ant. IV subdivided into two segments, asymmetrically arranged with Ant. IVa longer than IVb (Fig. 7E) (0.6 : 0.4, n = 4), without apical bulb (Fig. 7C). Lengths of antennal segments I to IV (IVa+IVb) as 1:1.7:2:2.7 (average, n = 4). Antennal chaetae (scales, 5 types of ordinary chaetae, 14 types of S-chaetae and subapical organit) described separately.

General chaetotaxy (Figs 2E, 3A–D). Body densely covered with oval scales; ventro-lateral scales larger than dorsal ones; posterior scales of tergites larger than anterior ones (17–59 μm long).

Dorsal macrochaetae formula: 4,2/9,4/0,2,4,3 (Figs 2E, 3A). Trichobothrial pattern : 1/0, 0/0, 2, 3, 3 (Figs 2E, 3A). Trichobothrial complexes well developed with modified mes of various sizes (Fig. 3A–D), described below for each segment. The figured mes pattern is not complete.

Head chaetotaxy. Head with 10–11 peri-antennal mac in line on each side, with 4+4 central mac (chaetae A, B, D, G of Deharveng and Gers (1993); AMS = A3, M2, M1 and S3), absence of the chaetae C, E and F. Cephalic mes short, feebly serrated, equal, 9+9 symmetrically arranged (Fig. 2E). One lateral cephalic trichobothria much shorter than the closest mac on each side; suture zone not visible (Fig. 2E). Head dorsally densely covered with round to oval scales (25–35 μm long).

Ventral chaetotaxy of head densely covered with oval scales (65–72 μm long), postlabial chaetae along the linea ventralis as 3 smooth mes anteriorly and 2 smooth chaetae laterally, one mac and an oblique line of 7–8 mes posteriorly on each side (Fig. 2H).

Tergite chaetotaxy. Th. II with a collar consisting of a few rows of mac along its anterior and antero-lateral margins, a compact group of 6 central mac on each side ("P3 complex" of Soto-Adames et al. (2014) and 3 antero-lateral mac; 1 antero-lateral ms; 1 antero-lateral sens; 3 short mic postero-laterally, and a few others not counted centrally (Fig. 3A).

Th. III with 4 mac by side (a group of 3 central and 1 anterior to them), 1 sens at antero-lateral margins, and about 16 mac or long mes at lateral margins (Fig. 3A).

Abd. I without central mac, with 1 ms laterally on each side, a row of 3 mics below psp, a6 (sensu Soto-Adames 2015) absent, and 5 mes laterally (Fig. 3A).

Abd. II with 2 tric on each side and 6 modified mes around them (2 around the internal tric and 3–4 near external tric), 2 mac (1 near internal tric and 1 near external tric), 1 sens near internal tric, 2 mic close to external tric), at least 6 other mes sockets visible at lateral margins (not drawn) (Fig. 3A, B).

Abd. III with 3 tric on each side (1 internal, 2 external) and 9–10 modified mes around tric (3 near internal tric, 6–7 near the two external tric); 4 mac (1 near internal

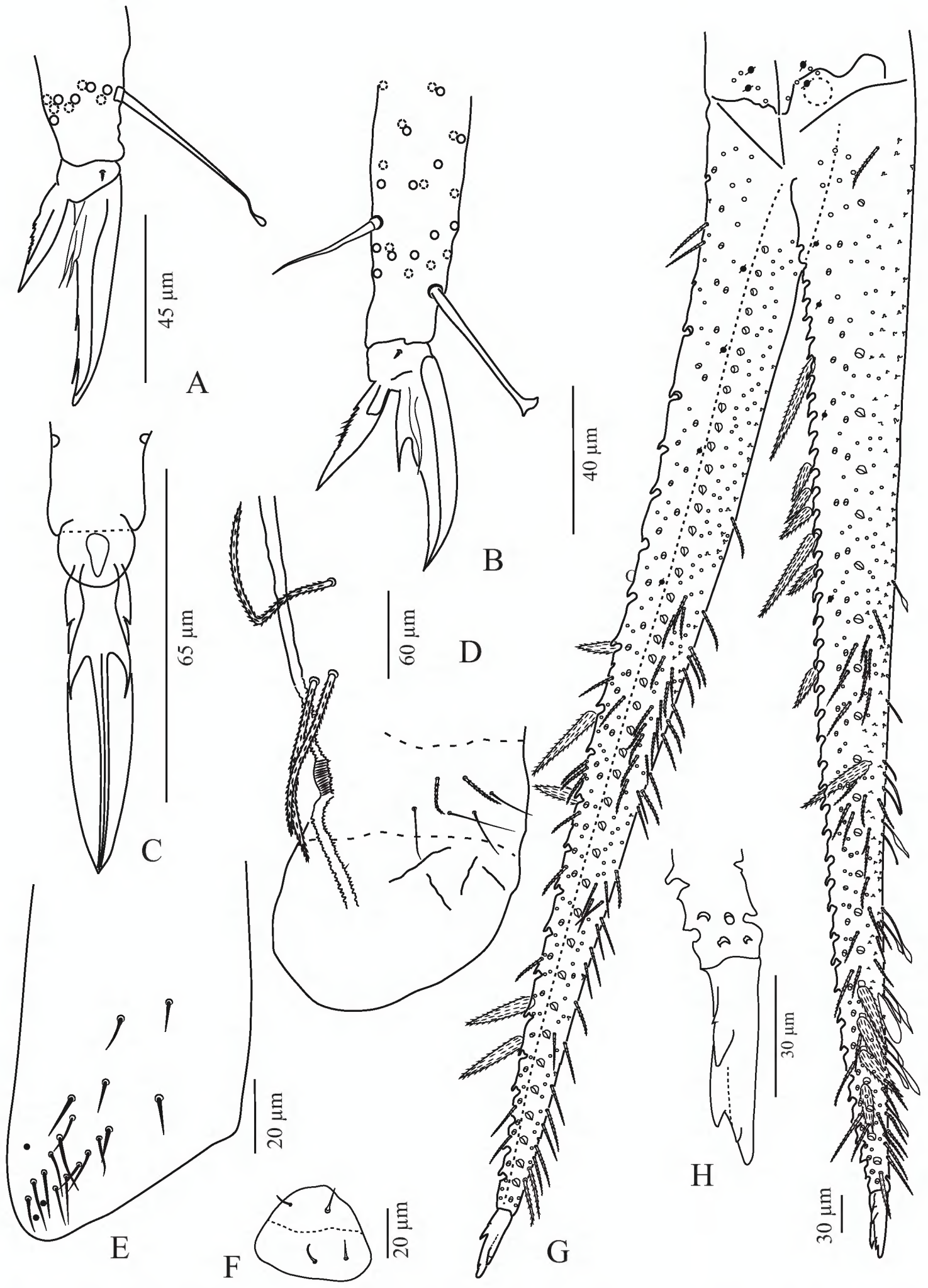

Figure 4. *Troglopedetes spectabilis* sp. nov., continued **A** distal part of tibiotarsus I and claw complex with clavate tenent hair **B** distal part of tibiotarsus III and claw complex with clavate tenent hair **C** ventral side of claw complex **D** lateral flap and antero-distal face of ventral tube **E** trochanteral organ **F** female genital plate **G** distal part of Manubrium and Mucrodens **H** mucro.

tric and 3 near external tric); 1 sens anterior to internal tric and ms not seen; at least 7 mes at lateral margins (Fig. 3A, C).

Abd. IV with 3 tric on each side (2 antero-lateral, 1 postero-lateral) and about 7–11 modified mes around the two antero-lateral tric; postero-lateral tric without modified mes. Mac distributed as 3 central on each side (1 antero-external to pseudopore, 2 anterior to posterior tergite margin), 1 near postero-lateral tric, and at least 4 external, mixed with at least 13 mes or smaller mac on lateral to posterior margins; 2 sens; at least 9 S-like chaetae sensu Lukić et al. (2015) anteriorly, and at least 5 mes or short S-like chaetae uniformly distributed; at least 3 serrated mes in line in the posterior row along pseudopore line, from medium to short size (Fig. 3A, D).

Abd. V with 2 sens detected on each side, and several ordinary chaetae from mes to mac, not counted (Fig. 3A). Abd. VI chaetotaxy not analyzed.

Legs (Fig. 4A–C). Legs long. Tita III 1.3–1.4 times longer than the head diagonal, slightly longer than Tita I and II. Legs devoid of scales, mostly covered with ordinary ciliated chaetae of various length, from mes to mac. Trochanteral organ of leg III with 19–21 smooth, straight, unequal spiny chaetae (n = 4) (Fig. 4E). Tibiotarsus chaetotaxy mostly composed of strong ciliated-serrated mes, the basal ones longer and thicker (52–69 μm), slightly shorter distally (up to 35–40 μm). Distal row with 9–10 subequal ciliated mes and a dorso-apical tenent hair clavate on tita; a ventro-distal strong smooth erected chaeta present on Tita III (Fig. 4B). Praetarsal mic minute (3.5–4 μm), clearly seen in one side (Fig. 4B). Unguis slender and long (56–66 μm long, 12–15 μm wide at basis), 10 times shorter than tita. Claw I and II with 2 strong unpaired inner teeth at 50–57% and 80–89%, and a pair of inner basal teeth of equal size (Fig. 4A); Claw III with a very tiny tooth at 88% of inner edge (Fig. 4B, C), outer edge with a minute tooth at 19–25% usually inconspicous; unguiculus pointed, narrow, lanceolate and elongate, 0.5–0.7 times shorter than the claw, its external edge with at least 9 toothlets (Fig. 4B).

Ventral tube (Fig. 4D). Ventral tube about 4 times longer than wide, with 3+3 long serrated mac anteriorly and 6 mes (2 ciliated and 4 smooth) on each lateral flap; posterior side not visible.

Furca complex (Fig. 4G, H). Tenaculum with 4 teeth on each ramus, of decreasing size from the basal to the distal one, on a prominent, irregular body, with a postero-basal strong, densely serrated, distally bent chaeta. Manubrium about 1.28 times (n = 5) shorter than the mucrodens (mucro+dens). Manubrium dorsally with subequal ciliated mes (none smooth), irregularly arranged in 3–4 rows in two longitudinal stripes separated by a glabrous axial stripe, external row of chaetae distally with at least 11 long ciliated mes, dorso-distal plaque with 4+4 mes and 2+2 pseudopores (Fig. 4G). Ventrally with a dense cover of round to oval (30–60 μm) and thin elongated scales (35–70 μm). Dens straight, elongate, hairy, slightly and progressively tapering, dorsally with 2 rows of spines, mixed with ciliated mes of various length, thickness and shape. Dorso-external row with 21–24 spines, dorso-internal row with 40–46 spines (asymmetries between dentes); external spines larger and less sclerotized than the internal ones. Some short ciliated mes interspersed with spines in the external row; dorsally

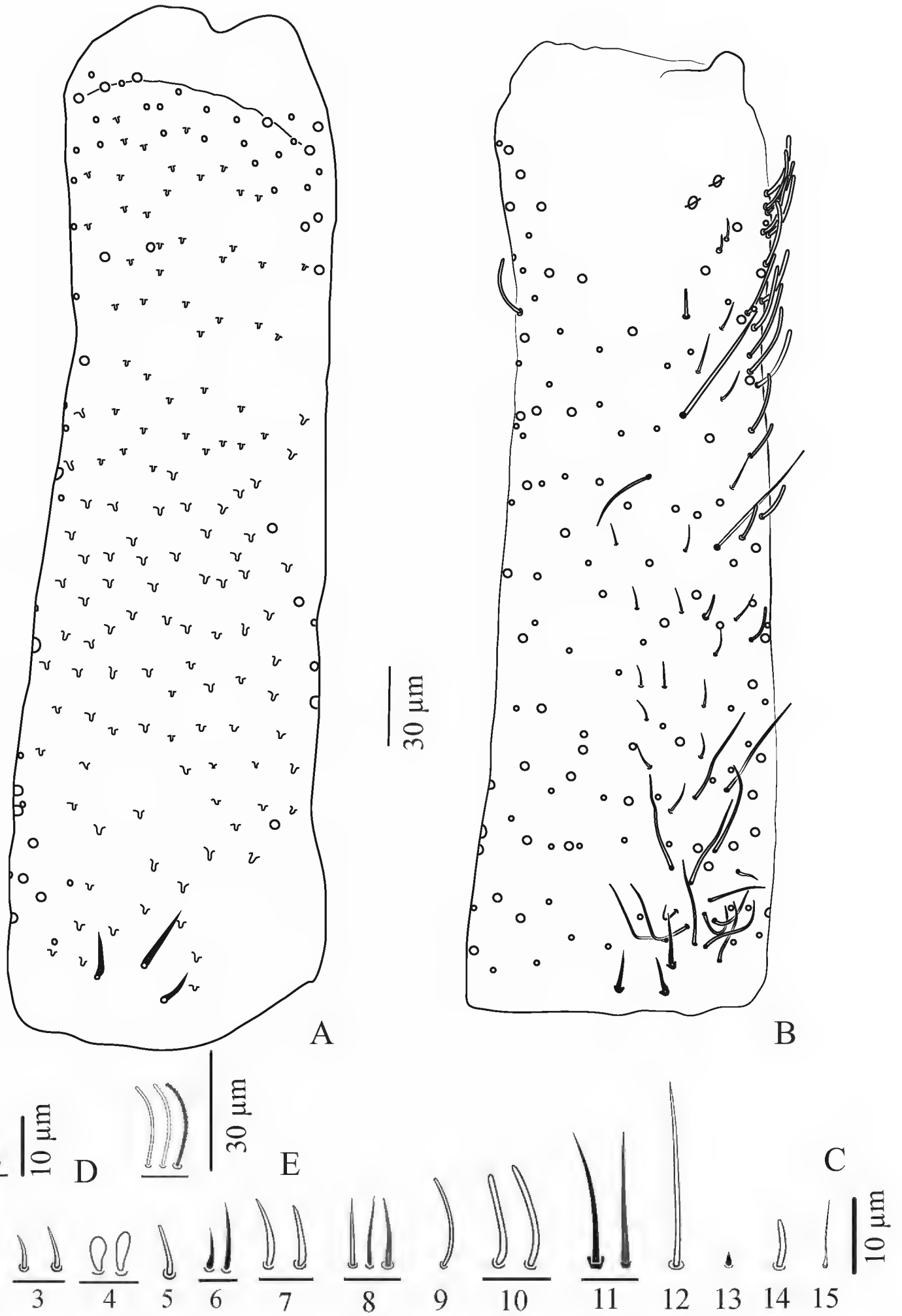

Figure 5. *Troglopedetes spectabilis* sp. nov., continued **A** dorsal side of Ant. I, right side **B** ventral side of Ant. I, right side **C** type of antennal S-chaetae **D** subapical organite of Ant. IV.

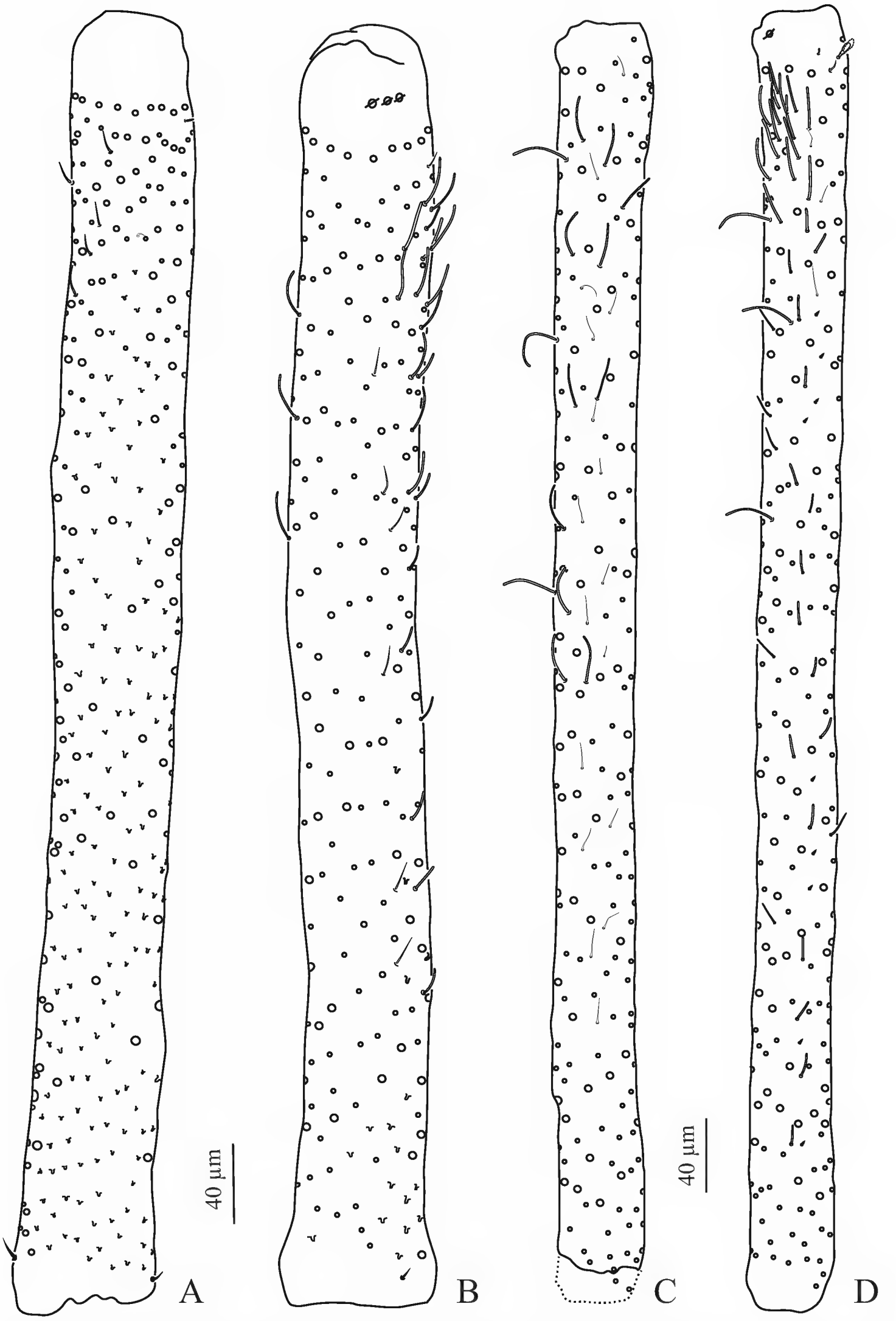

Figure 6. *Troglopedetes spectabilis* sp. nov., continued **A** dorsal side of Ant. II, right side **B** ventral side of Ant. II, right side **C** dorsal side of Ant. III, right side **D** ventral side of Ant. III, right side.

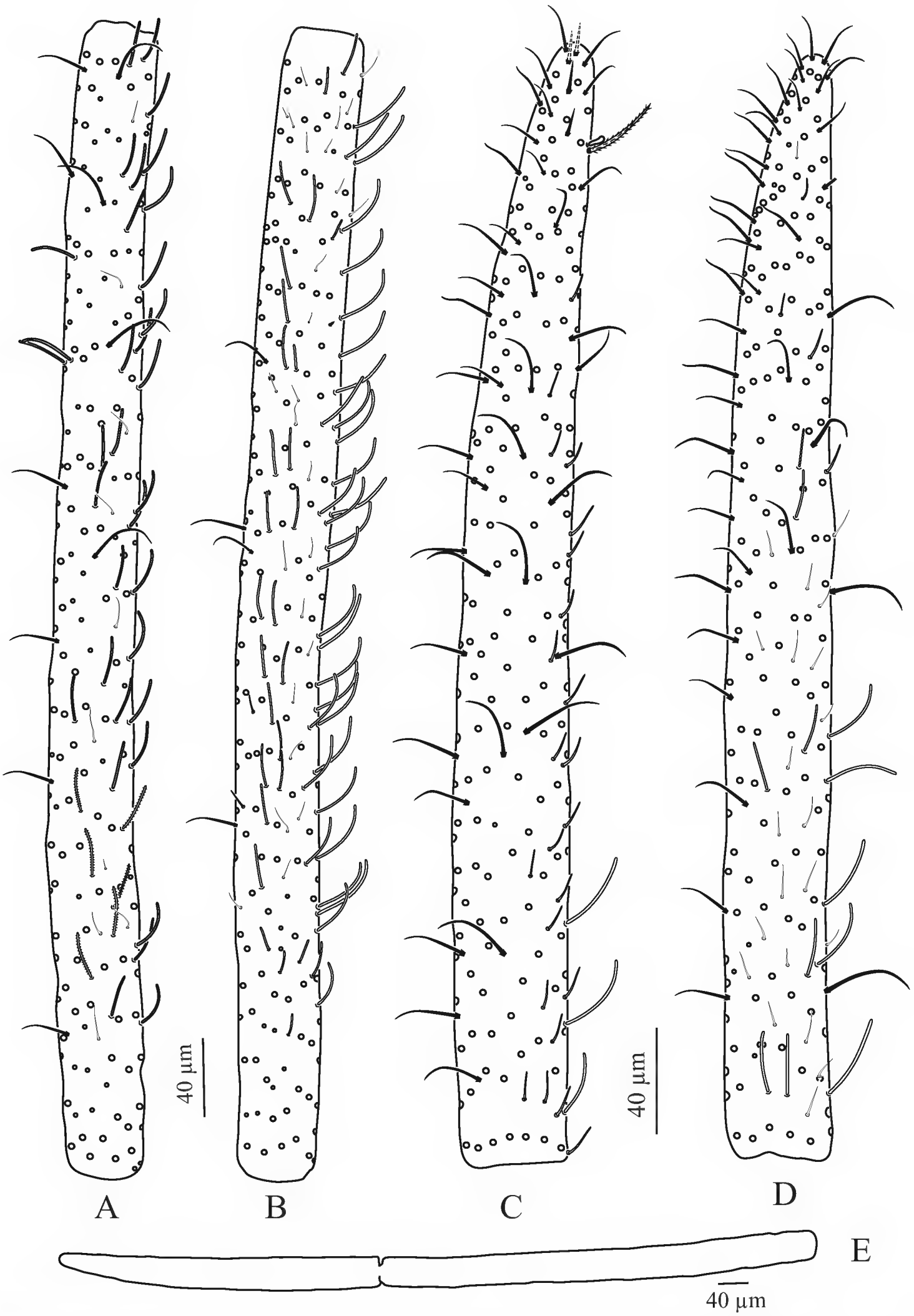

Figure 7. *Troglopedetes spectabilis* sp. nov., continued **A** dorsal side of Ant. IVa, right side **B** ventral side of Ant. IVa, right side **C** dorsal side of Ant. IVb with subapical organite, right side **D** ventral side of Ant. IVb, right side **E** Ant.IV with asymmetric subsegments, right side.

between the two rows of spines a mix of short and long ciliated mes, irregularly arranged in one row distally turning to 3–4 rows proximally; laterally, many short ciliated mes; dorso-distally, 3–(4) stronger ciliated mes; 4+4 psp on dorso-basally between the two rows of spine (Fig. 4G). Dens ventrally entirely and densely scaled, the scales elongate (25–60 µm) (oval shape distally), arranged in short lines from 3–5 (distally) to 6–8 scales (proximally) (Fig. 4G). Mucro rather stout, short, 13.5–14.4 (average 14, n = 5) times shorter than dens (Fig. 4G, H), with 4 main teeth, the apical one blunt and strong, the subapical one acute and strong, a latero-distal one small and acute, and 1 dorso-basal, minute, acute and strong, acute with one toothlet basally (Fig. 4H).

Genital plate (Fig. 4F). Female genital plate with 2+2 mic.

Ecology. *Troglopedetes spectabilis* sp. nov. exclusively inhabits a chamber in the dark zone of a cave. Specimens were found in an oligotrophic habitat with a very humid and wet environment on muddy ground. The air temperature in the chamber was 23.5–24.3 °C, soil temperature was 22.9–23.1 °C and the relative humidity was 84%. The cave is undisturbed and rather difficult to access (due to the steep slope up to the entrance). It is located in dry evergreen forest mixed with bamboo forest at moderate altitude (426 m. asl.). Some simple infastructure has been introduced into the cave, including a metal ladder at the entrance.

Etymology. The species name is derived from the Latin word *spectabilis*, meaning "remarkable" or "admirable" and referring to its extremely long antennae.

Remarks. *Troglopedetes spectabilis* sp. nov. is the most highly troglomorphic species of *Troglopedetes*. It is clearly distinct from other species of the genus by the extreme length of its appendages, especially the antennae (the ratio of antenna: head is 5.5), by its claw complex and by its furca (Table 1). Chaetae m2 and l1 of labial basis are smooth whereas they are ciliated in all other described species in the country. Central area of head has A, B, D, G macrochaetae. Dens of *T. spectabilis* sp. nov. is very long with 40–46 internal spines and 4 psp, while the other species of the genus in Thailand have only 2 psp. A most unexpected character of this species is the very different claw morphology of leg I–II and leg III checked in several specimens, which may have taxonomic and evolutionary implication that will be discussed in future works.

2. *Troglopedetes takensis* sp. nov.

http://zoobank.org/E85B3D17-ACCF-4F3F-9616-32F70190726F

Figs 8–13

Type locality. Thailand, Tak Province, Tha Song Yang district, Tham (cave) Mae Usu (17°18'15.0"N, 98°09'19.9"E, 172 m a.s.l.).

Type material. ***Holotype*:** female on slide, Tak Province: Tha Song Yang district, Tham (cave) Mae Usu, 17°18'15.0"N, 98°09'19.9"E, 145 m a.s.l., 7 March 2019, S. Jantarit, A. Nilsai and K. Jantapaso leg., dark zone of cave, by aspirator (sample # THA_SJ_TAK03). ***Paratypes*:** 5 paratypes on slides (all subadult), same locality and date as the holotype.

Table 2. *Troglopedetes takensis* sp. nov., measurements in μm (from paratype).

Head		Tergites		Appendages	
Ant. I	192	Th. II	200	Man	540
Ant. II	390	Th. III	212	Dens	580
Ant. III	390	Abd. I	110	Mucro	48
Ant. IVa	322	Abd. II	120	Furca	1,168
Ant. IVb	230	Abd. III	140	Claw I	62
Ant.	1,524	Abd. IV	655	Claw II	62
Head	465	Abd. V	80	Claw III	65
		Abd. VI	60		
		Body	1,577		

Holotype and 5 paratypes deposited in NHM-PSU, measurements of holotype in Table 2.

Description. ***Habitus.*** Troglomorphic, slender, with elongate legs, furca and antennae. Length: 1.9–2.0 mm (n = 4) (body 1.4–1.6 mm, head 0.4 mm). Fourth abdominal segment 4–5 times (n = 4) longer than the third one along the dorsal axis. Furca well developed, about 1.4–1.5 (n = 3) times shorter than the body length. Body colour white with spots of orange pigment. Eyes not detected, but with 2+2 pigmented ocular patches.

Chaetal types. Four types of chaetae on somites, appendages (except antennae) and mouthparts: scales, present on antennal segment I and II, head, body and ventral side of the furca, absent on legs and ventral tube; ordinary chaetae on all body parts; S-chaetae and trichobothria on tergites; hairs devoid of sockets on outer maxillary lobe. Chaetal types on antennae are much more diverse and described separately further.

Pseudopores (Figs 8A, 9A–D, 11B). Pseudopores present as round flat disks larger than mac sockets, on antennae, head and tergites. Head pseudopore sometimes present aymmertrically on one side only. Dorsal pseudopore formula: 1/1, 1/1, 1, 1, 1+4 (Figs 8A, 9A–D). On antenna, 1 psp detected ventro-distally on Ant. I (Fig. 11B), without psp on Ant. II and Ant. III. On head, 1 psp close to antennal basis (Fig. 8A). On legs, psp present externally on coxae (1–(2) for legs I and II and 2 for leg III). On manubrium, 2 psp on the dorso-distal plaque; on each dens, 2 psp dorso-basally near the internal spine row.

Mouthparts. Clypeus with 13 large mes, symmetrically arranged: 9 ciliated posteriorly and 4 thin smooth anteriorly (Fig. 8F). Labral formula 4/5,5,4 (Fig. 8E); prelabral chaetae short, bent and ciliated, labral chaetae thinner, longer, smooth and acuminate, those of the distal row slightly larger and longer than those of the median row; the anterior line not concave in V or U-shape. Ventro-distal complex of labrum well differentiated, asymmetrical, with 2 distal combs (a larger one with 8–9 teeth on the left side, a smaller one with 13–14 minute teeth on the right side) and an axial pair of sinuous tubules. Distal part of labrum not adorned with spines dorso-distally. Labial palp similar to that described by Fjellberg (1999) for *Troglopedetes* sp., with strong papillate chaetae. Number of guards for each major papillate chaetae: A (0), B (5), C (0), D (4) and E (4); lateral process subcylindrical, surpassing the apex of papilla E (Fig. 8B); 5 proximal chaetae. Chaetae of labial basis as M1M2REL1l2, with M1, M2, R, E, L1 subequal and ciliated, l2 short, smooth and acuminate (Fig. 8G).

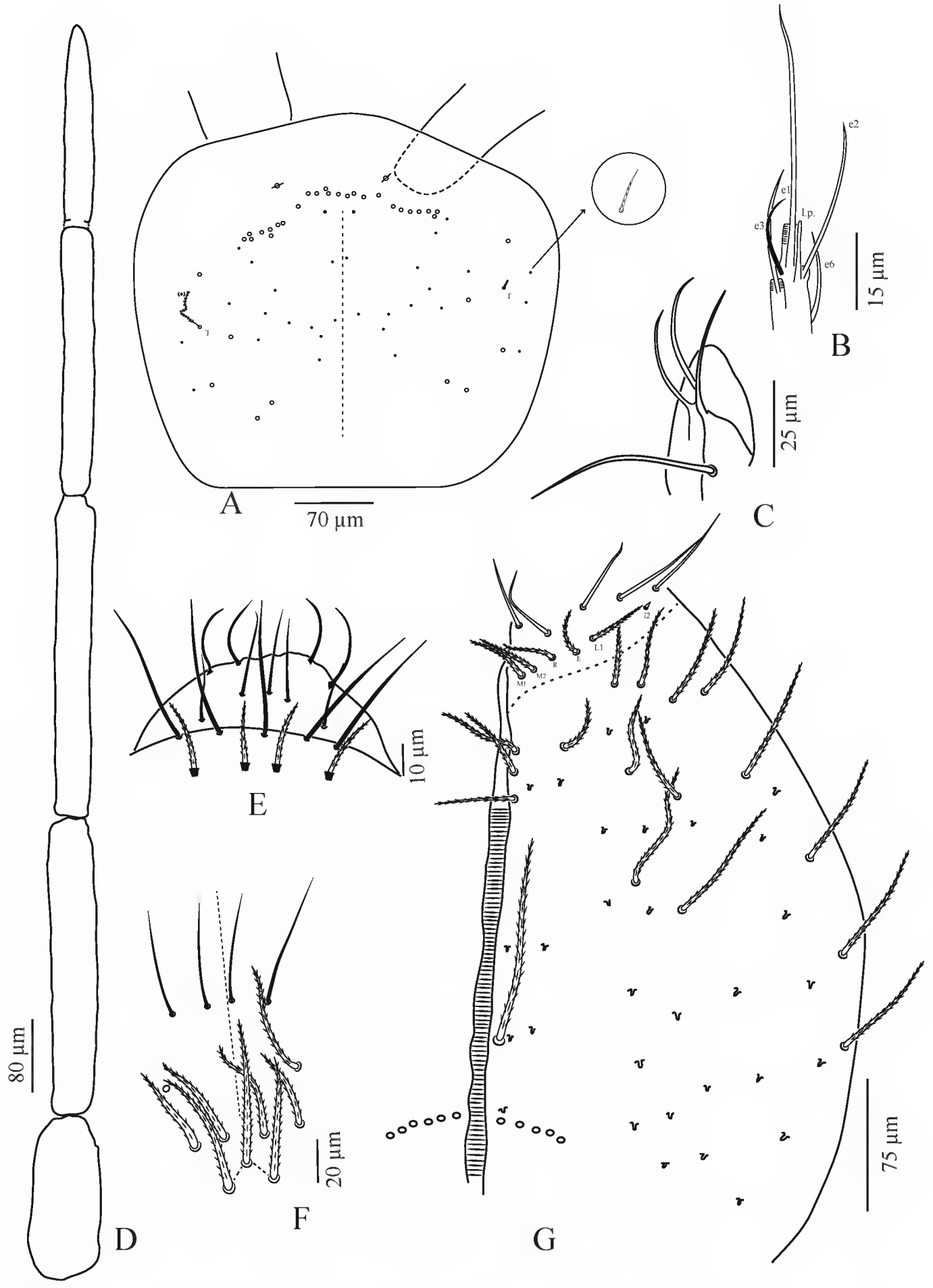

Figure 8. *Troglopedetes takensis* sp. nov. **A** head chaetotaxy **B** papilla E of labial palp **C** outer maxillary lobe **D** antenna **E** labrum **F** clypeus **G** labial basis and ventral chaetotaxy of head, right side.

Outer maxillary lobe with 1 papillate chaeta, 1 basal chaeta longer than the others and 2 sublobal hairs (Fig. 8C). Maxillary head with a 3-toothed claw, several stout shortly ciliated lamellae not observed in detail and 2 thin elongate structures (1 dorsally and 1 ventrally). Mandible head strong, asymmetrical (left side with 4 teeth, right side with

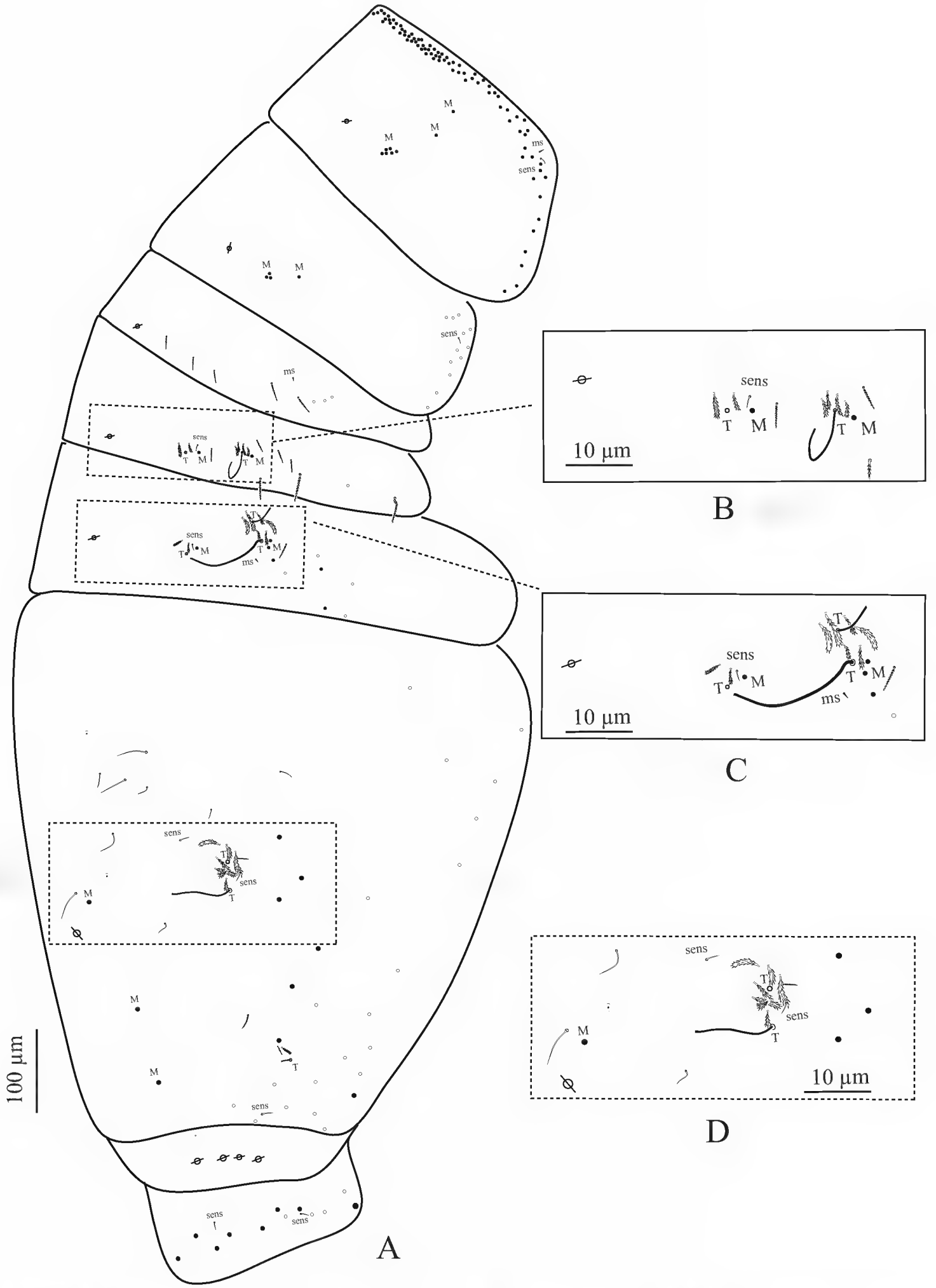

Figure 9. *Troglopedetes takensis* sp. nov., continued **A** chaetotaxy of tergites **B** trichobothrial complexes of Abd. II **C** trichobothrial complexes of Abd. III **D** trichobothrial complex of Abd. IV.

5); molar plate with 3 strong pointed basal teeth, and other 2–3 inner distal teeth, identical in both mandibles.

Antennae (Figs 11–13). Antennae elongated (1,274–1,524 μm, n = 4), slightly shorter than body+head length (n = 3), and 3.2 times (n = 4) longer than the cephalic diagonal. Ant. IV subdivided into two segments, asymmetrically arranged with Ant. IVa longer than IVb (0.57 : 0.43, n = 4), without apical bulb (Fig. 13D). Lengths of antennal segments I to IV (IVa+IVb) as 1:1.9:1.9:3 (average, n = 4). Antennal chaetae (scales, 5 types of ordinary chaetae, 13 types of S-chaetae and subapical organit) described separately.

General chaetotaxy (Figs 8A, 9A–D). Body scales densely covered with oval scales; ventro-lateral scales larger than the dorsal ones; posterior scales of tergites larger than the anterior ones (24–40 μm long).

Dorsal macrochaetae formula: 0,2/8,4/0,2,4,3 (Figs 8A, 9A). Trichobothrial pattern : 1/0, 0/0, 2, 3, 3 (Figs 8A, 9A). Trichobothrial complexes well developed with modified mes of various sizes (Fig. 9A–D) described below for each segment. The figured mes pattern not complete.

Head chaetotaxy (Fig. 8A, G). Head with 11–14 peri-antennal mac in line on each side, no central mac. Cephalic mes short, feebly serrated, equal, 15+15 symmetrically arranged (Fig. 8A). One lateral cephalic trichobothria much shorter than the closest mac on each side; suture zone not visible (Fig. 8A).

Head dorsally densely covered with round to oval scales (33–45 μm long). Ventral chaetotaxy of head densely covered with oval scales (57–67 μm long), postlabial chaetae along the linea ventralis as ciliated mes anteriorly and 3 ciliated chaetae laterally, one mac and an oblique line of 5–6 mes posteriorly on each side (Fig. 8G).

Tergite chaetotaxy (Fig. 9A–D). Th. II with a collar consisting of a few rows of mac along its anterior and antero-lateral margins, a compact group of 6 central mac on each side and 2 antero-lateral mac; 1 antero-lateral ms; 1 antero-lateral sens, mes to mic not counted centrally (Fig. 9A).

Th. III with 4 mac by side (a group of 3 central and 1 anterior to them), 1 sens at antero-lateral margins, and about 12 mac or long mes at lateral margins (Fig. 9A).

Abd. I without central mac, with 1 ms laterally on each side, a row of 3 mics below psp, a6 absent, and 5 mes laterally (Fig. 9A).

Abd. II with 2 tric on each side and 6 modified mes around them (2 around the internal tric and 4 near external tric), 2 mac (1 near internal tric and 1 near external tric), 1 sens near internal tric, 4 mic (1 close to internal tric and 3 close to external tric), at least 3 other mes at lateral margins (Fig. 9A, B).

Abd. III with 3 tric on each side (1 internal, 2 external) and 8 modified mes around tric (2 near internal tric, 6 near the two external tric); 4 mac (1 near internal tric and 3 near external tric); 1 sens anterior to internal tric and 1 ms; at least 5 mes to small mac at lateral margins (Fig. 9A, C).

Abd. IV with 3 tric on each side (2 antero-lateral, 1 postero-lateral) and about 7 modified mes around the two antero-lateral tric; postero-lateral tric with 1 modified

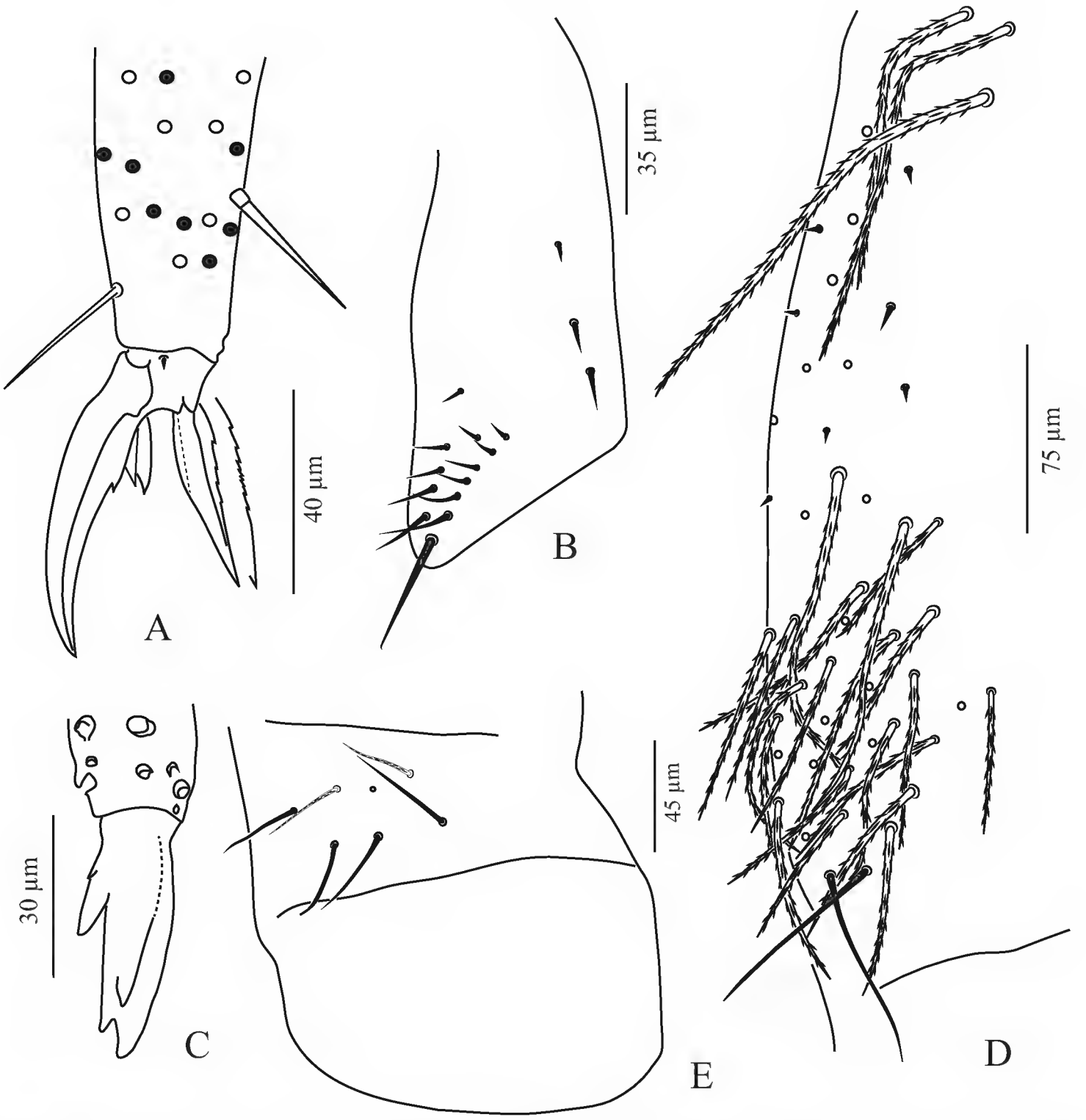

Figure 10. *Troglopedetes takensis* sp. nov., continued **A** distal part of tibiotarsus III and claw complex with pointed tenent hair **B** trochanteral organ **C** mucro **D** posterior side of ventral tube **E** lateral flap of ventral tube.

mes. Mac distributed as 3 central on each side (1 antero-external to pseudopore, 2 anterior to posterior tergite margin), 1 near postero-lateral tric, and at least 5 external, mixed with at least 14 mes or smaller mac on lateral to posterior margins; 3 sens; at least 4 S-like chaetae sensu Lukić et al. (2015) anteriorly, and at least 5 mes or short S-like chaetae uniformly distributed; at least 1 serrated mes in line in the posterior row along pseudopore line (Fig. 9A, D).

Abd. V with 2 sens detected on each side, and several ordinary chaetae from mes to mac, not counted (Fig. 9A). Abd. VI chaetotaxy not analyzed.

Legs (Fig. 10A, B). Legs long. Tita III as long as the head diagonal, slightly longer than Tita I and II. Legs devoid of scales, mostly covered with ordinary ciliated chaetae

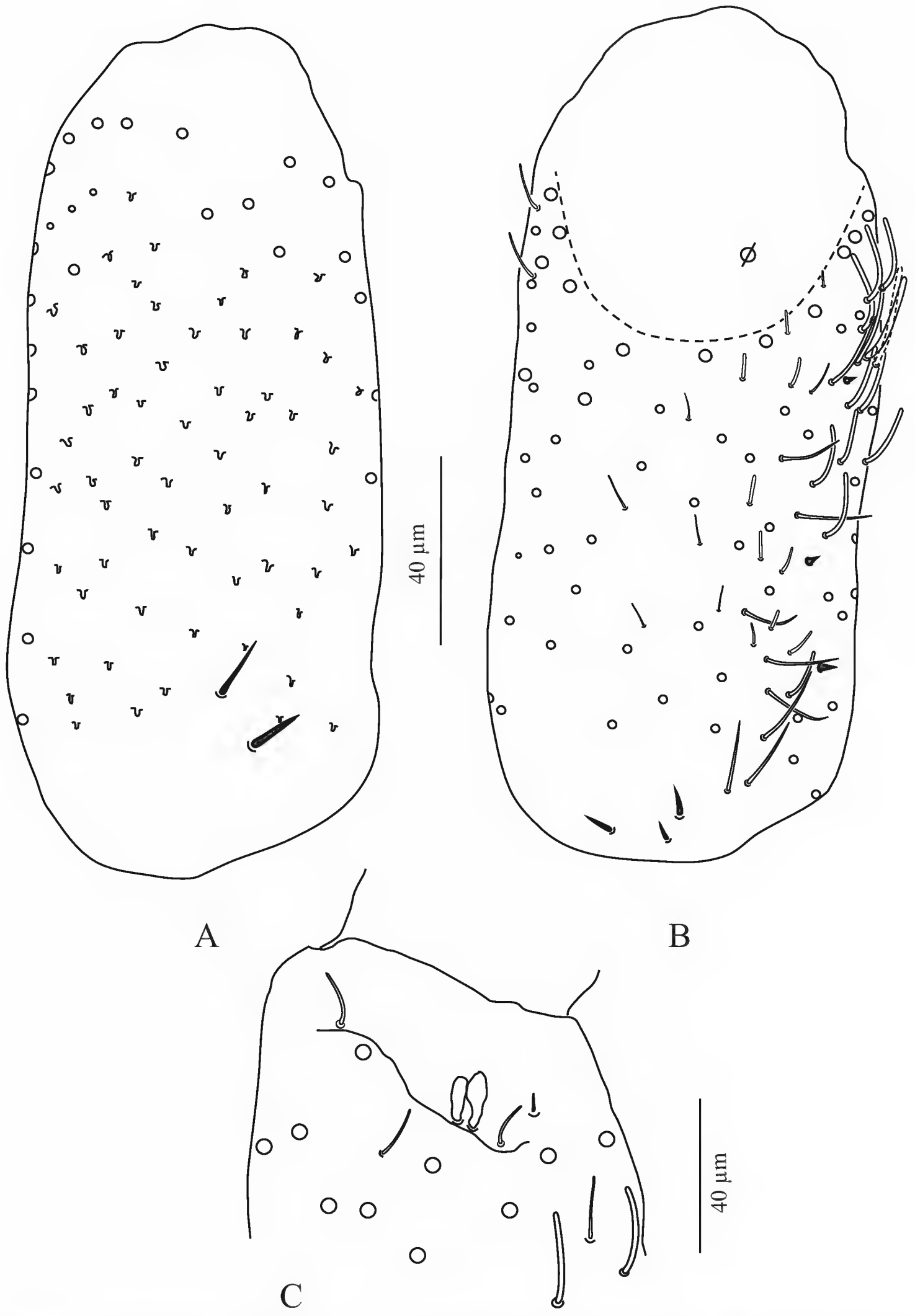

Figure 11. *Troglopedetes takensis* sp. nov., continued **A** dorsal side of Ant. I, left side **B** ventral side of Ant. I, left side **C** distal organ of Ant.III, right side.

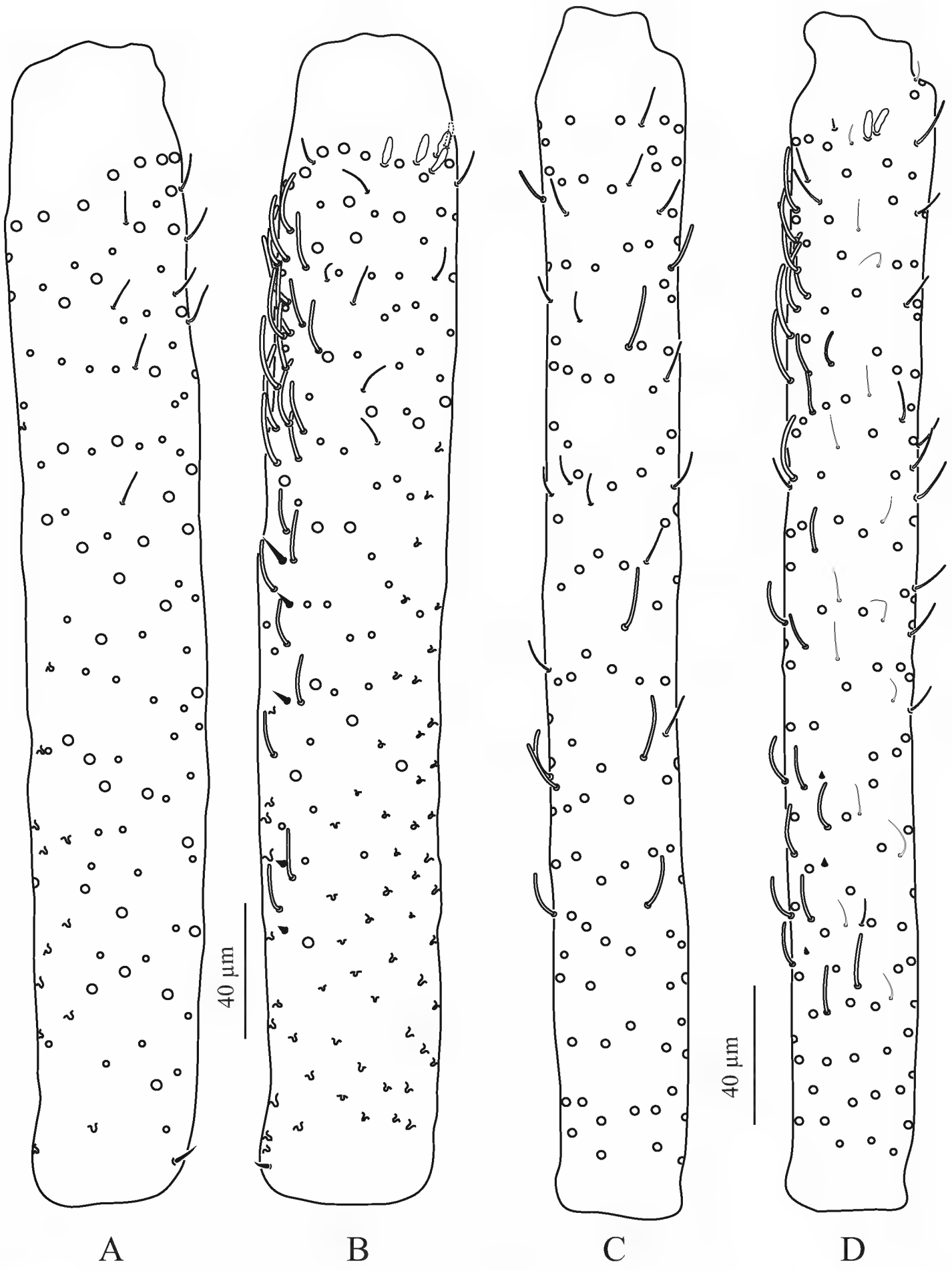

Figure 12. *Troglopedetes takensis* sp. nov., continued **A** dorsal side of Ant. II, left side **B** ventral side of Ant. II, left side **C** dorsal side of Ant. III, left side **D** ventral side of Ant. III, left side.

of various length, from mes to mac. Trochanteral organ of leg III with 15–17 smooth, straight, unequal spiny chaetae (n = 3) (Fig. 10B). Tibiotarsus chaetotaxy mostly composed of strong ciliated-serrated mes, the basal ones longer and thicker (50–70 µm), slightly shorter distally (up to 35–45 µm). Distal row with 7–9 subequal ciliated mes

and a dorso-apical tenent hair thin, pointed on all tita; a ventro-distal strong smooth erected chaeta present on Tita III (Fig. 10A). Praetarsal mic minute (3.5–4 μm), clearly seen in one side (Fig. 10A). Unguis in all legs slender and long (60–65 μm long, 13 μm wide at basis), 7 times shorter than tita, with a pair of inner basal teeth of equal size, one uneven inner basal tooth, outer edge with a minute tooth at 20–23% usually inconspicous; unguiculus pointed, narrow, lanceolate and elongate, about 0.6–0.7 times shorter than the claw, its external edge irregular with at least 4–9 toothlets (Fig. 10A).

Ventral tube (Fig. 10D, E). Ventral tube about 3.8 times longer than wide, with 3+3 long serrated mac anteriorly and 7 mes (3 ciliated and 4 smooth) on each lateral flap (Fig. 10E); posterior side with at least 39 ciliated mes, 2 smooth mes and 7 small spines (Fig. 10D).

Furca complex (Fig. 10C). Tenaculum with 4 teeth on each ramus, of decreasing size from the basal to the distal one, on a prominent, irregular body, with a postero-basal strong, densely serrated, distally bent chaeta. Manubrium about 1.13 times (n = 4) shorter than the mucrodens (mucro+dens). Manubrium dorsally with subequal ciliated mes (none smooth), irregularly arranged in 3–4 rows in two longitudinal stripes separated by a glabrous axial stripe, external row of chaetae distally with at least 11–19 long ciliated mac, dorso-distal plaque with 4+4 mes and 2+2 pseudopores. Ventrally with a dense cover of round to oval (25–57 μm long) and thin elongated scales (25–40 μm long). Dens straight, elongate, hairy, slightly and progressively tapering, dorsally with 2 rows of spines, mixed with ciliated mes of various length, thickness and shape. Dorso-external row with 23–28 spines, dorso-internal row with 33–40 spines (asymmetries between dentes); external spines larger and less sclerotized than the internal ones. Some short ciliated mes interspersed with spines in the external row; dorsally between the two rows of spines a mix of short and long ciliated mes, irregularly arranged in one row distally turning to 3–4 rows proximally; laterally, many short ciliated mes; dorso-distally, 3–(4) stronger ciliated mes; 2+2 psp on dorso-basally between the two rows of spine. Dens ventrally entirely and densely scaled, the scales elongate (15–27 μm long) (oval shape distally), arranged in short lines from 3–5 (distally) to 6–8 scales (proximally). Mucro rather stout, short, 10.6–12.1 (n = 4) times shorter than dens, with 4 main teeth, the apical one blunt and strong, the subapical one acute and strong, a latero-distal one small and acute, and 1 dorso-basal, minute, acute and strong, with one toothlet basally (Fig. 10C).

Ecology. *T. takensis* sp. nov. is only known from a large chamber in the dark zone of a cave. Specimens were found as small populations in an oligotrophic habitat, i.e. on the wall and ground surface, with a very humid and wet environment, with small trace of organic matter. Air temperature in the chamber was 22.2–23.0 °C, soil temperature was 21.9 °C and the relative humidity was 85%.

Etymology. The species name is derived from the name of the province (Tak) where it was found.

Remarks. *Troglopedetes takensis* sp. nov. has elongated antennae (the ratio of antenna: head is 3.2), legs and furca (Table 2), but shorter than in *T. spectabilis* sp. nov. It presents two distinct black small eye-patches on each side and lacks central mac on the head. Claws usually have only one uneven inner basal tooth (with 2 specimens without

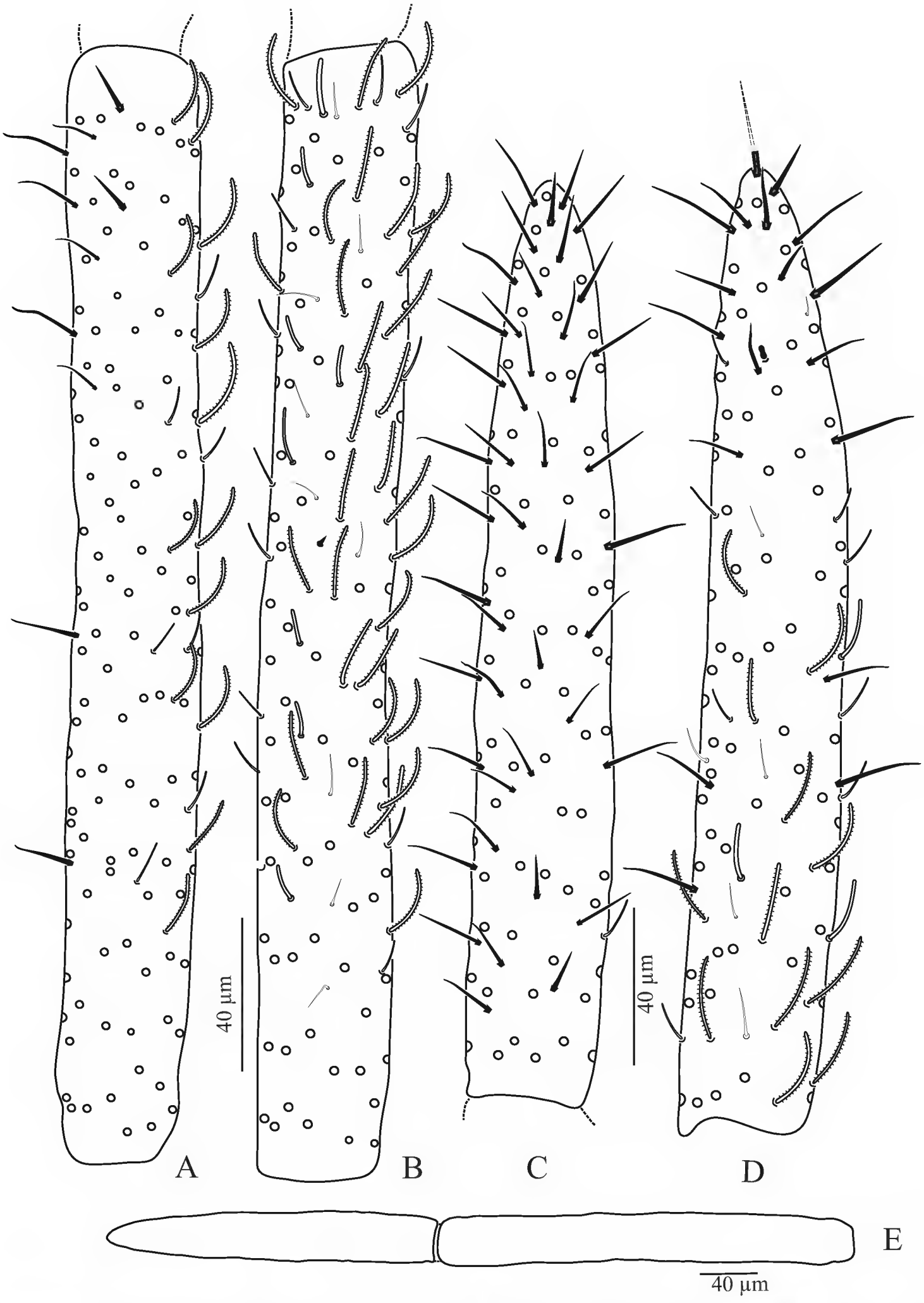

Figure 13. *Troglopedetes takensis* sp. nov., continued **A** dorsal side of Ant. IVa, left side **B** ventral side of Ant. IVa, left side **C** dorsal side of Ant. IVb, left side **D** ventral side of Ant. IVb with subapical organite, left side **E** Ant.IV with asymmetric subsegments, left side.

uneven inner tooth on claw III). *T. takensis* sp. nov. shares with *T. calvus* Deharveng & Gers, 1993 the absence of central mac on head. However, the new species differs from *T. calvus* in size (1.9–2.0 vs 0.9–1.4), presence of eyes-patches (2+2 vs 0), length of antenna (1,274–1,524 μm vs 747 μm), tenent hair (pointed vs clavate), inner teeth of claw ((0)1 vs 2), internal row of dental spines (33–40 vs 14–32).

3. *Troglopedetes rungsimae* sp. nov.

http://zoobank.org/FBDC2D39-F7CB-4920-98E0-F2DEDC7E91F7
Figs 14, 15

Type locality. Thailand, Kanchanaburi Province, Sai Yok district, Tham (cave) Khang Khao (14°11'23.8"N, 98°59'37.0"E, 262 m a.s.l).

Type material. ***Holotype*:** male on slide, Kanchanaburi Province: Sai Yok district, Tham (cave) Khang Khao, 14°11'23.8"N, 98°59'37.0"E, 262 m a.s.l., 28 February 2019, S. Jantarit, A. Nilsai and K. Jantapaso leg., dark zone of cave, by aspirator (sample # THA_SJ_KRI11). ***Paratypes*:** 2 subadults on slides, same locality and date as the holotype.

Holotype and 2 paratypes deposited in NHM-PSU, measurements of holotype in Table 3.

Description. ***Habitus.*** Troglomorphic, slender, with elongate legs, furca and antennae. Length: 1.2–1.3 mm (n = 3) (body 0.9–1.0 mm, head 0.2–0.3 mm). Fourth abdominal segment 4–5 times (n = 3, 1 male and 2 subadults) longer than the third one along the dorsal axis. Furca well developed, about 1.4–1.5 (n = 3) times shorter than body length. Body colour white with spots of orange pigment. Eyes absent, no ocular patch.

Chaetal types. Four types of chaetae on somites, appendages (except antennae) and mouthparts: scales, present on antennal segment I and II, head, body and ventral side of the furca, absent on legs and ventral tube; ordinary chaetae on all body parts; S-chaetae and trichobothria on tergites; hairs devoid of sockets on outer maxillary lobe. Chaetal types on antennae are much more diverse and described separately further.

Table 3. *Troglopedetes rungsimae* sp. nov., measurements in μm (from holotype).

Head		Tergites		Appendages	
Ant. I	95	Th. II	128	Man	340
Ant. II	240	Th. III	120	Dens	338
Ant. III	210	Abd. I	70	Mucro	37
Ant. IVa	200	Abd. II	80	Furca	715
Ant. IVb	160	Abd. III	90	Claw I	30
Ant.	905	Abd. IV	430	Claw II	32
Head	260	Abd. V	70	Claw III	32
		Abd. VI	45		
		Body	1,033		

Pseudopores (Figs 14C, 15A–D). Pseudopores present as round flat disks larger than mac sockets, on antennae, head and tergites. Dorsal pseudopore formula: 1/1, 1/1, 1, 1, 1+4 (Figs 14C, 15A–D). On antenna, 1 psp detected ventro-distally on Ant. I, 1 psp on Ant. II, Ant. III and Ant.IVb. On head, 1 psp close to antennal basis (Fig. 14C). On legs, psp present externally on coxae (1 for legs I and 2 for legs II and III). On manubrium, 2 psp on the dorso-distal plaque; on each dens, 2 psp dorso-basally near the internal spine row

Mouthparts. Clypeus not visible. Labral formula 4/5,5,4; prelabral chaetae short, bent and ciliated, labral chaetae thinner, longer, smooth and acuminate, those of the distal row slightly larger and longer than those of the median row; the anterior line not cleary seen. Ventro-distal complex of labrum well differentiated, asymmetrical, with 2 distal combs (a larger one with 9–10 teeth on the left side, a smaller one with 10–12 minute teeth on the right side) and an axial pair of sinuous tubules. Distal part of labrum not adorned with spines dorso-distally. Labial palp similar to that described by Fjellberg (1999) for *Troglopedetes* sp., with strong papillate chaetae. Number of guards for each major papillate chaetae: A (0), B (5), C (0), D (4) and E (4); lateral process subcylindrical, surpassing the apex of papilla E (Fig. 14B); 5 proximal chaetae. Chaetae of labial basis as M1M2REL1l2, with M1, M2, E and L1 subequal and ciliated, R shorter than others and ciliated, l2 short, smooth and acuminate (Fig. 14D). Outer maxillary lobe with 1 papillate chaeta, 1 basal chaeta and 2 sublobal hairs (Fig. 14A). Maxillary head with a 3-toothed claw, several stout shortly ciliated lamellae not observed in detail and 2 thin elongate structures (1 dorsally and 1 ventrally). Mandible head strong, asymmetrical (left side with 4 teeth, right side with 5); molar plate with 3 strong pointed basal teeth, and other 2–3 inner distal teeth, identical in both mandibles.

Antennae. Antennae (743–905 μm, n = 3), shorter than body+head length (n = 3), 3.1 times (n = 3) longer than the cephalic diagonal. Ant. IV subdivided into two segments, asymmetrically arranged with Ant. IVa longer than IVb (0.57 : 0.43, n = 3), without apical bulb. Length of antennal segments I to IV (IVa+IVb) as 1:2.4:2.2:3.6 (n = 2). Antennal chaetae (scales, 5 types of ordinary chaetae, 13 types of S-chaetae and subapical organit).

General chaetotaxy (Figs 14C, 15A–D). Body scales densely covered with round to oval scales, the scales in ventro-lateral is larger than the dorsal side and posterior scales of tergites larger than the anterior ones (20–40 μm long). Dorsal macrochaetae formula: 3,4/8,4/0,2,4,3 (Figs 14C, 15A). Trichobothrial pattern : 1/0, 0/0, 2, 3, 3 (Figs 14C, 15A). Trichobothrial complexes well developed with modified mes of various sizes (Fig. 15A–D) described below for each segment. The figured mes pattern is not complete.

Head chaetotaxy (Fig. 14C, D). Head with 12–13 peri-antennal mac in line on each side, with 3+3 central mac (chaetae A, C and E); AMS = A3, S5 and S3), absence of the chaetae B, D, F and G. Cephalic mes short, feebly serrated, equal, 10+10 symmetrically arranged (Fig. 14C). One lateral cephalic trichobothria much shorter than the closest mac on each side; suture zone not visible (Fig. 14C). Head dorsally densely covered with round to oval scales (25–45 μm long). Ventral chaetotaxy of head densely

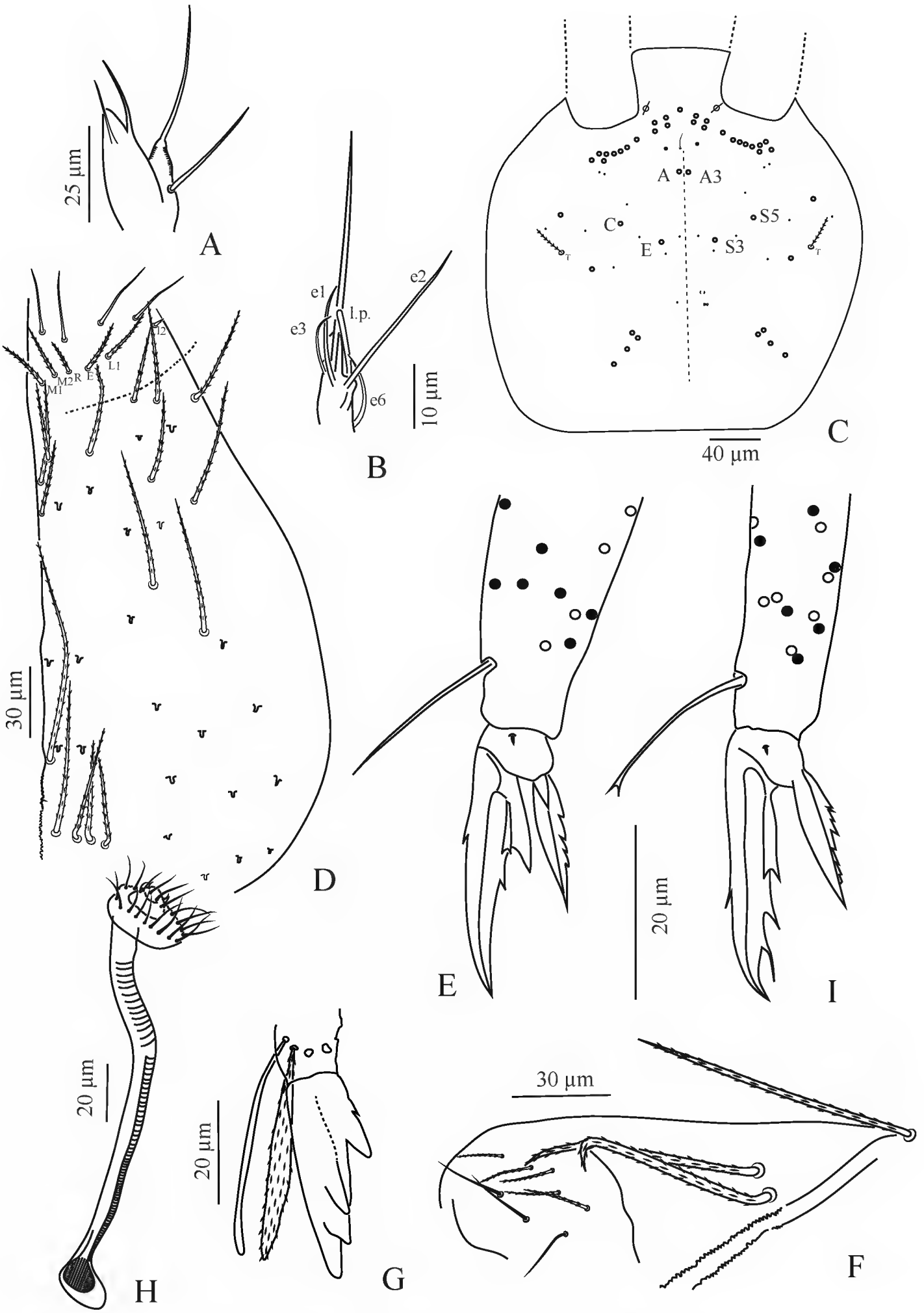

Figure 14. *Troglopedetes rungsimae* sp. nov. **A** outer maxillary lobe **B** papilla E of labial palp **C** head chaetotaxy (left = A to G mac nomenclature; right = AMS nomenclature) **D** labial basis and ventral chaetotaxy of head, right side **E** distal part of tibiotarsus III and claw complex **F** lateral flap of ventral tube **G** mucro **H** male genital plate **I** distal part of tibiotarsus III and claw complex with clavate tenent hair of an undescribed species co-occurring with *T. rungsimae* sp. nov.

covered with oval scales (40–50 μm long), postlabial chaetae along the linea ventralis as ciliated mes anteriorly and 3 ciliated chaetae laterally, one mac and an oblique line of 4 mes posteriorly on each side (Fig. 14D).

Tergite chaetotaxy (Fig. 15A–D). Th. II with a collar consisting of a few rows of mac along its anterior and antero-lateral margins, a compact group of 6 central mac on each side and 2 antero-lateral mac; 1 antero-lateral ms; 1 antero-lateral sens, and other mes not counted centrally (Fig. 15A).

Th. III with 4 mac by side (a group of 3 central and 1 anterior to them), 1 sens at antero-lateral margins, and about 9 mac or long mes at lateral margins (Fig. 15A).

Abd. I without central mac, with 1 ms laterally on each side, a row of 3 mics below psp, a6 absent, and 5 mes laterally (Fig. 15A).

Abd. II with 2 tric on each side and 7 modified mes around them (2 around the internal tric and 5 near external tric), 2 mac (1 near internal tric and 1 near external tric), 1 sens near internal tric (Fig. 15A, B), 3 mic (1 close to internal tric and 2 close to external tric), at least 1 other mes socket at lateral margins.

Abd. III with 3 tric on each side (1 internal, 2 external) and 7 modified mes around tric (2 near internal tric, 5 near the two external tric); 4 mac (1 near internal tric and 3 near external tric); 1 sens anterior to internal tric and 1 ms; at least 6 mic to mes at lateral margins (Fig. 15A, C).

Abd. IV with 3 tric on each side (2 antero-lateral, 1 postero-lateral) and about 7 modified mes around the two antero-lateral tric; postero-lateral tric with 1 modified mes. Mac distributed as 3 central on each side (1 antero-external to pseudopore, 2 anterior to posterior tergite margin), 1 near postero-lateral tric, and at least 5 external, mixed with at least 13 mes or smaller mac on lateral to posterior margins; 3 sens; at least 5 S-like chaetae sensu Lukić et al. (2015) anteriorly, and at least 2 mes or short S-like chaetae uniformly distributed; at least 1 serrated mes in line in the posterior row along pseudopore line (Fig. 15A, D).

Abd. V with 2 sens detected on each side, and several ordinary chaetae from mes to mac, not counted (Fig. 15A). Abd. VI chaetotaxy not analyzed.

Legs (Fig. 14E). Legs long. Tita III as long as the head diagonal, slightly longer than Tita I and II. Legs devoid of scales, mostly covered with ordinary ciliated chaetae of various length, from mes to mac. Trochanteral organ of leg III with 13 smooth, straight, unequal spiny chaetae. Tibiotarsus chaetotaxy mostly composed of strong ciliated-serrated mes, the basal ones longer and thicker (33–48 μm), slightly shorter distally (up to 20–34 μm). Distal row with 8 subequal ciliated mes and a dorso-apical tenent hair thin, smooth and pointed; a ventro-distal strong smooth erected chaeta present on Tita III. Praetarsal mic minute (2.5–3 μm), present in both sides. Unguis slender and long (29–38 μm long, 7 μm wide at basis), 8.9 times shorter than tita, with one inner tooth, and a pair of inner basal teeth of unequal size, outer edge with a minute tooth at 40–42%; unguiculus pointed, narrow, lanceolate and elongate, about 0.6–0.7 time shorter than the claw, its external edge with at least 4 toothlets (Fig. 14E).

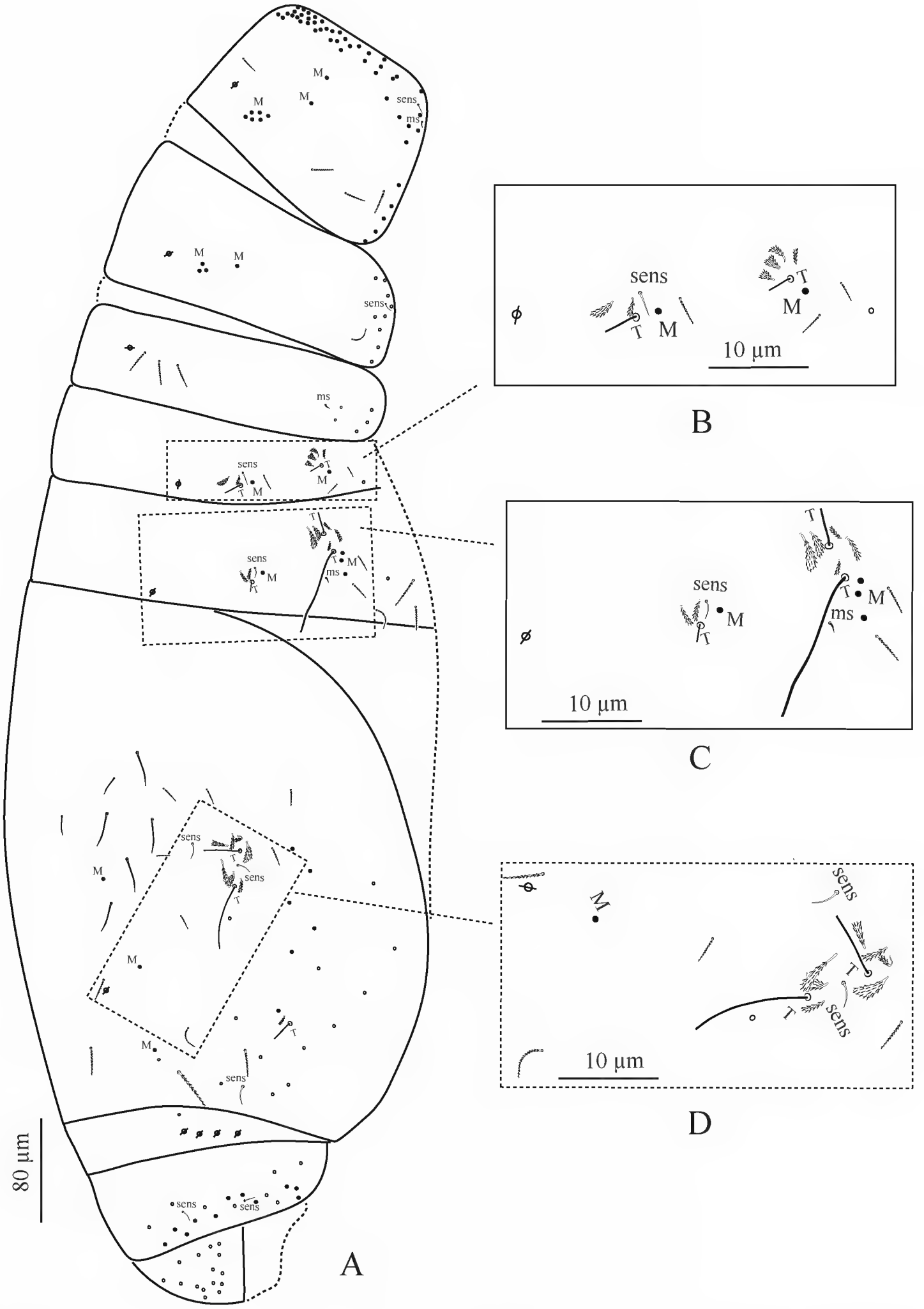

Figure 15. *Troglopedetes rungsimae* sp. nov., continued **A** chaetotaxy of tergites **B** trichobothrial complexes of Abd. II **C** trichobothrial complexes of Abd. III **D** trichobothrial complex of Abd. IV.

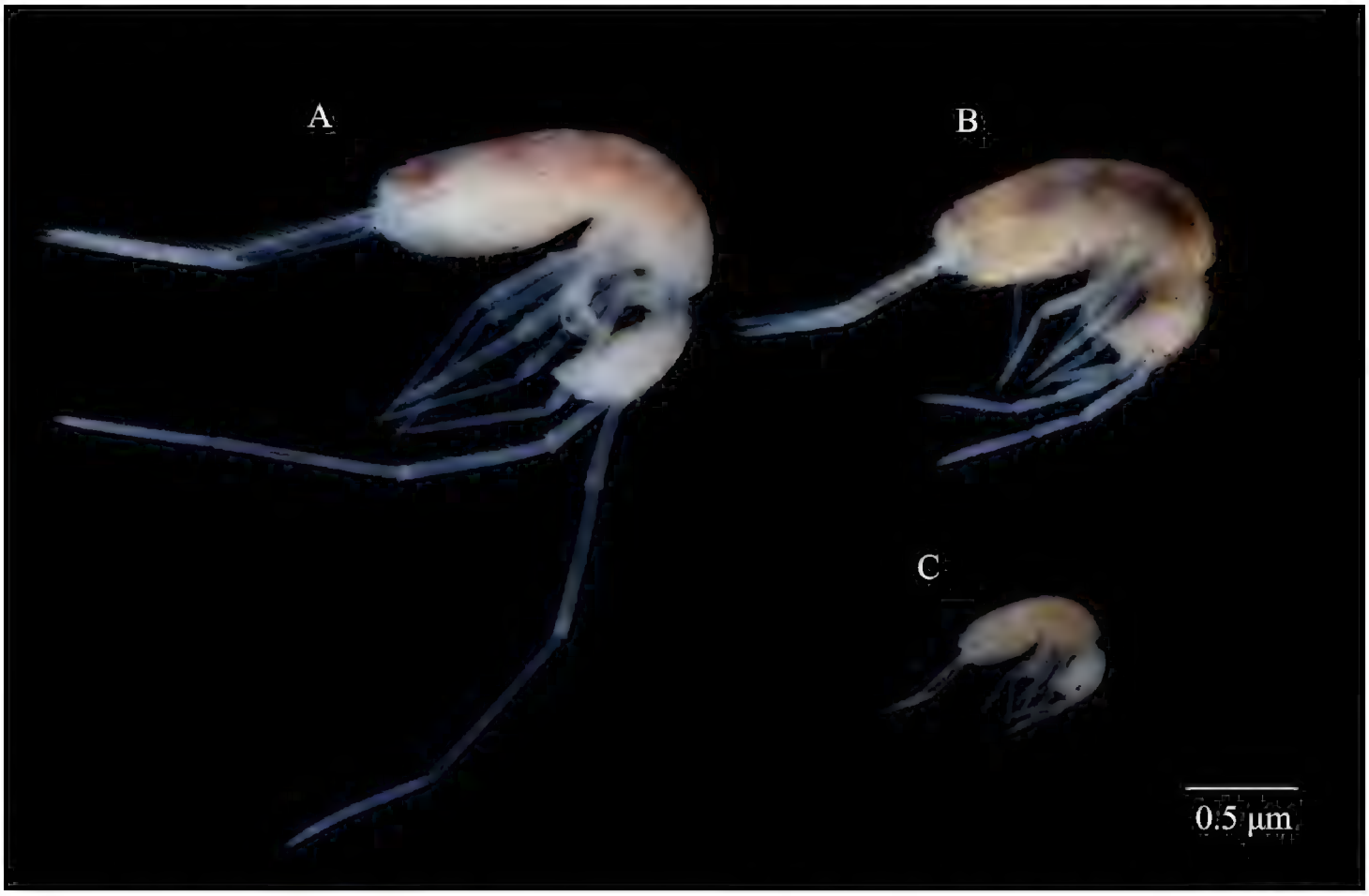

Figure 16. Troglomorphic traits (appendage elongation and body size) in Thai species of the genus *Troglopedetes* **A** highly troglomorphic species *T. spectabilis* sp. nov., where Ant.II and III are fused together **B** troglomorphic form of an undescribed species **C** non-troglomorphic form of an undescribed species with eyes and eyes patch.

Ventral tube (Fig. 14F). Ventral tube about 3.1 times longer than wide, with 3+3 long serrated mac anteriorly and 8 mes (5 ciliated and 3 smooth) on each lateral flap; posterior side not visible (Fig. 14F).

Furca complex. Tenaculum with 4 teeth on each ramus, of decreasing size from the basal to the distal one, on a prominent, irregular body, with a postero-basal strong, densely serrated, distally bent chaeta. Manubrium about 1.13 times (n = 3) shorter than mucrodens (mucro+dens). Manubrium dorsally with subequal ciliated mes (none smooth), irregularly arranged in 3–4 rows in two longitudinal stripes separated by a glabrous axial stripe, external row of chaetae distally with at least 10 long ciliated mac, dorso-distal plaque with 4+4 mes and 2+2 pseudopores. Ventrally, with a dense cover of round to oval (15–25 µm long) and thin elongated scales (25–30 µm long). Dens straight, elongate, hairy, slightly and progressively tapering, dorsally with 2 rows of spines, mixed with ciliated mes of various length, thickness and shape. Dorso-external row with 16–18 spines, dorso-internal row with 29 spines (asymmetries between dentes); external spines larger and less sclerotized than the internal ones. Some short ciliated mes interspersed with spines in the external row; dorsally between the two rows of spines a mix of short and long ciliated mes, irregularly arranged in one row distally turning to 3–4 rows proximally; laterally, many short ciliated mes; dorso-distally, 3–(4) stronger ciliated mes; 2+2 psp on dorso-basally between the two rows of spine. Dens

ventrally entirely and densely scaled, the scales elongate (25–40 μm long) (oval shape distally), arranged in short lines from 3–5 (distally) to 6–8 scales (proximally). Mucro rather stout, short, 8.9–9.2 (n = 3) times shorter than the dens, with 4 main teeth, the apical one blunt and strong, the subapical one acute and strong, a latero-distal one small and acute, and 1 dorso-basal, minute, acute and strong, with one toothlet basally (Fig. 14G).

Genital plate (Fig. 14H). Male genital plate with 19 mic around the edge and 4 mic inside (Fig. 14H)

Ecology. *Troglopedetes rungsimae* sp. nov. is only known from a small chamber in the dark zone of a cave. Specimens were found as small populations in an oligotrophic habitat, i.e. on the wall and ground with a very humid and wet environment, without any trace of organic matter. Air temperature in the chamber where specimens were collected was 23.5–24.8 °C, soil temperature was 23.1–23.3 °C and relative humidity was 88–91%.

Etymology. The species is named in honour of Rungsima Tanthalakha, the Senior Program Director, Research Management and Innovation Management, National Science and Technology Develoment Agency, Thailand, who is interested in karst and cave biodiversity and for her contributions to the study of cave *Troglopedetes* in Thailand.

Remarks. *Troglopedetes rungsimae* sp. nov. has the sixth most elongated antennae of the *Troglopedetes* species of Thailand (Table 3) after *T. spectabilis* sp. nov., *T. multispinosus* Deharveng & Gers, 1993, *T. longicornis* Deharveng & Gers, 1993, *T. takensis* sp. nov. and *T. microps* Deharveng & Gers, 1993. It is similar to *T. dispersus* Deharveng & Gers, 1993 (which has been recorded from two caves in Kanchanaburi province: Tham Lawa and Tham Kaew), in the absence of eyes, and the dorsal macrochaetotaxy of the central head (with A, C, E mac). However, it differs from it by its longer antennae (almost 1 versus 0.6 time shorter than the body), outer maxillary lobe chaetotaxy (1 vs 2), chaetae on lateral flap of the ventral tube (8+8 versus 7+7), and higher ratio of dens: mucro (9.1 vs 8.5).

In the same cave, we found another morphotype with a different claw morphology. This type has thin, smooth and clavate tenent hair on all tita (one pointed on Claw I). Claw is long and slender with 2 strong inner teeth, one tooth at 57–73% of inner edge and the other at a 90–91% of inner edge, and a pair of inner basal teeth of unequal size. One small tooth is at 40% on the outer edge. Unguiculus is pointed, narrow, lanceolate and elongate, about 0.65 time shorter than the claw, and its external edge is with 7 toothlets (Fig. 14I). However, its dorsal chaetotaxy is the same as *T. rungsimae* sp. nov. Unfortunately, the material available is not sufficient to described it in detail.

Distribution of the genus *Troglopedetes* in Thailand and Southeast Asia

The genus *Troglopedetes* in Thailand is dominant in the subterranean environment in the northern and western regions and is present in the mountain range bordering Myanmar (unpublished data). It is also spread over a wide area of the central plain region where karst is extremely fragmented (Fig. 1). *Troglopedetes* is rarely found in the southern pen-

insula where only two recently described species are known (Jantarit et al. 2020). These are the only records of the genus from south of the Kra Isthmus, a hypothetical zoogeographical boundary that was earlier thought to separate the two closely related genera *Troglopedetes* and *Cyphoderopsis* Carpenter, 1917 (Deharveng 1987; Deharveng and Bedos 2001). The genus *Cyphoderopsis*, apart from the species found in India and Nepal, remains restricted to the south of the Kra Isthmus from the Thai-Malay peninsula to Western Indonesia, with a small number of species described (Jantarit et al. 2013). Interestingly, *Troglopedetes* is not present in the east and northeast regions of Thailand (Fig. 1), although many caves have been sampled there. The long Phetchabun-Dong Phaya Yen-Sankamphaeng mountain range, which stretches approximately north to south between the central plain and northeast region of Thailand, may have acted as a barrier to limit the dispersion of the genus *Troglopedetes* in Thailand. The genus is absent from the caves of southern Cambodia (unpublished data) and southern Vietnam (Deharveng et al. 2001), where it is replaced by the radiation of another Paronellidae genus, *Lepidonella* Yosii, 1960 (Deharveng and Bedos 1995). At least one undescribed species of *Troglopedetes* is reported from Luang Prabang in Laos (Besson et al. 2001), at a similar latitude to Mae Sai district, Chiang Rai province in northern Thailand, which is the northernmost record of the genus in Thailand. The large gaps in our knowledge of the countries surrounding Thailand obviously needs to be filled to provide a decent overview of the distribution limits of the genus in Southeast Asia.

Cave *Troglopedetes* in Thailand exhibit various degrees of adaption to cave life (troglomorphy), from a small set of morphological modifications to a complete set of darkness adaptions, as is also presented in the genus *Coecobrya* Yosii, 1956 (Jantarit et al. 2019). Two types of morphology are recognized among Thai *Troglopedetes* (Fig. 16). The first form is characterized by short appendages, short and rather swollen claw, small size (0.6–1.2 mm), and eyes and/or ocular patches generally present (Fig. 16C). Species of this form are usually associated with eutrophic habitats, especially guano piles, and are never troglomorphic. The second form has long to very long appendages (antennae, legs and furca), eyes are generally absent, slender claws and body size usually larger (1.3–2.2 mm) (Fig. 16A, B). Species of this form are mostly linked to oligotrophic cave habitats in wet and moist environments. They are very rare, with only six described species so far (*T. spectabilis* sp. nov., *T. multispinosus*, *T. longicornis*, *T. takensis* sp. nov., *T. microps* and *T. rungsimae* sp. nov.). However, some individuals of these species can also be found in guano patches in the dark zone of caves. Cave *Troglopedetes* of both morphological types all have very limited distribution ranges in Thailand.

Antennal phaneres

Phanere types and their arrangement pattern on each antennal segment that we recognised in the three new species are homologised and compared with the two species currently described from Thailand (*T. meridionalis* and *T. kae*, see details in Jantarit et al. 2020). A total of four kinds of antennal phaneres are recognised in Thai *Troglopedetes*, as described in Jantarit et al. (2020): scales, ordinary chaetae, S-chaetae and

the subapical organite of Ant. IV. In finer detail, there is one type of scale, 5 types of ordinary chaetae and 15 types of S-chaetae. A total of 22 types can therefore be recongnized based on morphological grounds.

For the scales (see Jantarit et al. 2020), only an oval shape (15–50 μm Í 7–30 μm) is found on antennae, present dorsally only on Ant. I (19–127 scales) and II (25–152 scales) and ventrally on Ant. II (16–127 scales), absent ventrally on Ant. I, and absent on Ant. III and IV (Fig. 3A, C, D, Table 4, 5)

Regarding ordinary chaetae, the five types mentioned above are present in the new species and their position is the same as described by Jantarit et al. (2020); figure not provided here).

The subapical organite of Ant. IV is short, thick, dark, swollen at the tip (4 μm) with protecting chaeta, inserted dorso-internally ca. 38–47 μm from the apex (Figs 7C, 13D).

With reference to the S-chaetae (sensu Deharveng 1983), they are present on all antennal segments, with a variety of thickness, shape and size (from mic to mes in size, 2–46 μm). According to Jantarit et al. (2020), 14 types (type 1–14) of S-chaetae are described in *T. kae* and 13 types (type 1–13) in *T. meridionalis*. In this study, 14 types were found in *T. spectabilis* sp. nov. (type 1–6, 8–15), 13 types in *T. takensis* sp. nov. (type 1–6, 8–13, 15) and in *T. rungsimae* sp. nov. (type 1–13). A total of 15 S-chaetae types are now recognized in the antennae of Thai *Troglopedetes*. Extreme diversity of antennal S-chaetae is therefore retrieved in all species examined so far, and comprises the same types of chaetae, as only a single new type has been detected (type 15) which is found exclusively in the elongated antennae of *T. spectabilis* sp. nov. and *T. takensis* sp. nov. The types 1 to 14 are described in the study of Jantarit et al. (2020), and characterized below; their position on antennae is given in Table 4.

- Type 1–minute mic, thin, pointed and dark (3–4 μm) (Fig. 5C1).
- Type 2–short mic, thin, usually bent and dark mic (6–12 μm) (Fig. 5C2).
- Type 3–short mic, thin, rather curved apically and hyaline (5–7 μm) (Fig. 5C3).
- Type 4–short, hyaline and swollen mic (foliaceous sens) (5–7 μm) (Fig. 5C4).
- Type 5–short, thin, bent, hyaline mic (sometimes looks dark) (6–10 μm) (Fig. 5C5).
- Type 6–short, thin, erected and dark mic (10–22 μm) (Fig. 5C6).
- Type 7–rather long, bent, hyaline mic, thinner distally and broad basally (7–14 μm) (Fig. 5C7).
- Type 8–rather long, thin, erected and hyaline mic (sometimes looking dark) (17–15 μm) (Fig. 5C8).
- Type 9–long, subcylindrical, bent, hyaline mic (15–21 μm) (similar to type 10 but smaller and thinner) (Fig. 5C9).
- Type 10–long, subcylindrical, bent, hyaline and rather broad mic (12–30 μm) (Fig. 5C10).
- Type 11–long, thin, erected and dark mic (10–27 μm) (Fig. 5C11).
- Type 12–long, thin and hyaline mic (20–46 μm) (Fig. 5C12).
- Type 13– minute, pointed and dark mic (3–9 μm) (Fig. 5C13).

- Type 14– rather short, subcylindrical, bent, hyaline (6 μm) (Fig. 5C14).
- Type 15– (a new type) thin, rather long, hyaline (7–18 μm) (Fig. 5C15).

Diversity and distribution patterns of antennal phaneres

The number of antennal phanneres used for the analysis and comparison in this study was observed from the holotype of each species. We counted a total of 741 to 2,183 chaetae per antenna for the 5 studied species of Thai *Troglopedetes*, including 207–485 S-chaetae, 483–1,402 ordinary chaetae, 48–295 scales and a single subapical organite (Tables 4 and 5). Overall, 2,183, 1,227 and 1,107 antennal chaetae were recorded in *T. spectabilis* sp. nov., *T. takensis* sp. nov. and *T. rungsimae* sp. nov. respectively. On a single antenna, 485 S-chaetae were numbered for *T. spectabilis* sp. nov., 308 for *T. takensis* sp. nov. and 348 for *T. rungsimae* sp. nov. Likewise, ordinary chaetae on a single antenna numbered 1,402 for *T. spectabilis* sp. nov., 790 for *T. takensis* sp. nov. and 687 for *T. rungsimae* sp. nov.

The ventral side of the antenna is richer in chaetae and S-chaetae than the dorsal side (overall = 1,042 versus 846 in *T. spectabilis* sp. nov.; 605 versus 494 in *T. takensis* sp. nov. and 528 versus 507 in *T. rungsimae* sp. nov.; S-chaetae = 320 versus 166 in *T. spectabilis* sp. nov.; 212 versus 96 in *T. takensis* sp. nov. and 195 versus 153 in *T. rungsimae* sp. nov. (Tables 4 and 5). Ordinary chaetae are more numerous on the ventral than on the dorsal side in *T. spectabilis* sp. nov. (722 versus 680), but in similar number in *T. takensis* sp. nov. and *T. rungsimae* sp. nov. (ordinary chaetae = 393 versus 398, and 333 versus 354 respectively).

The distribution of the different types of S-chaetae along with the antennal segments is arranged in more or less clearly defined patterns which are described below, compared with *T. meridionalis* and *T. kae* in the following paragraphs, summarised in Tables 4 and 5, and illustrated in Figures 5–7, 11–13.

First antennal segment: eight types of S-chaetae can be recognised (Figs 5A, B, 11A, B): type 3, type 5, type 6, type 8, type 9, type 10, type 12 and type 13 (type 13 is found exclusively in *T. takensis* sp. nov.). Only one type is present on the dorsal side (type 6), the others are located on the ventral side.

Second antennal segment: nine types of S-chaetae can be recognised (Figs 6A, B, 12A, B): type 2, type 3, type 4, type 6, type 7, type 8, type 10, type 13 and type 14. Three types are present on the dorsal and ventral side (type 2, type 4 and type 8). Three types on the dorsal side (type 3, type 6 and type 14) and three types on the ventral side (type 7, type 10 and type 13).

Third antennal segment: eight types of S-chaetae can be recognised (Figs 6C, D, 12C, D): type 1, type 4, type 5, type 7, type 8, type 13, type 10 and type 15. They are present on the dorsal and ventral side except type 13 which is only present on the ventral side. AIIIO has typically 5 S-chaetae: one chaeta of type 1, two chaetae of type 4 and two chaetae of type 5 (Figs 6C, D, 11C, 12D).

Fourth antennal segment: nine types of S-chaetae can be recognised (Figs 7A–D, 13A–D): type 1, type 4, type 7, type 8, type 9, type 10, type 11, type 13 and type 15.

All are present on the dorsal and ventral side, except two types (1 and 9) that are present on the ventral side only and one type (7) that is present on the dorsal side only. They are distributed as follows on each subsegment.

Fourth antennal segment I (a): seven types of S-chaetae can be recognised: type 1, type 8, type 9, type 10, type 11, type 13, type 15. They are present on the dorsal and ventral side, except two types (1 and 9) that are present on the ventral side only.

Fourth antennal segment II (b): six types of S-chaetae can be recognised: type 4, type 7, type 8, type 10, type 11 and type 15. They are present on the dorsal and ventral side, except one type (7) that is present on the dorsal side only and one type (15) that is present on the ventral side only.

The most frequent antennal S-chaetae are type 8 (from 65 to 137 chaetae) and type 10 (from 36 to196 chaetae), which are present along all antennal segments. The other types are specific to three, two or a single segment(s) (Table 4, 5). A new type (type 15) is found exclusively on the extremely long antennae of *T. spectabilis* sp. nov. and *T. takensis* sp. nov. on Ant. III and IV and is absent in *T. rungsimae* sp. nov., *T. kae* and *T. meridionalis*.

With regard to the abundance of S-chaetae along antennal segments, the result for the new species is similar to that in *T. meridionalis* and *T. kae* where type 8 is the most common followed by type 11 and 10 (Tables 4 and 5). Likewise, Ant. IV has the highest number of S-chaetae in all the new species followed by Ant. III, I and II in *T. spectabilis* sp. nov., and followed by Ant. III, II and I in *T. takensis* sp. nov. and *T. rungsimae* sp. nov. (Table 5), while ordinary chaetae abundance ranks as Ant. IV, III, II and I in *T. spectabilis* sp. nov. and *T. takensis* sp. nov. and Ant. IV, II, III and I in *T. rungsimae* sp. nov. (Table 5).

The distal subsegment of antenna IV (Ant. IVb) is richer in S-chaetae than the proximal subsegment (Ant. IVa) in *T. takensis* sp. nov. and *T. rungsimae* sp. nov., but the number of S-chaetae is similar in *T. spectabilis* sp. nov.. The ordinary chaetae are more numerous in the proximal subsegment (Ant. IVa) than in the distal subsegment (Ant. IVb) in *T. takensis* sp. nov. and *T. rungsimae* sp. nov., but the number is rather similar in *T. spectabilis* sp. nov. (Table 5).

Comparison of the diversity of antennal chaetae between the three new species, *Troglopedetes* kae and *T. meridionalis*

Antennal chaetotaxy in Thai *Troglopedetes* is clearly plurichaetotic and extremely complex. Overall 22 types of antennal chaetae have been recognized. They are ordinary chaetae (5 types), S-chaetae (15 types), the subapical organite of Ant. IV and scales. According to Jantarit et al. (2020), 12 chaetal types were located at fixed positions on antennal segments. However, with the 3 additional species from this study considered in addition to *T. meridionalis* and *T. kae* described in Jantarit et al. (2020), fixed positions of antennal chaetae are left for only 7 types. They are 4 types of ordinary mes (type 1–4); 3 types of S-chaetae (type 11, 12) and the subapical organite of Ant. IV (Tables 4 and 5). Their diversity and distribution on the antennae are rather similar between

Table 4. Detailed distribution of antennal chaetae in the three new species and in *T. meridionalis* and *T. kae*.

Type of chaetae	Distribution on antenna	Location	Position on antennal segment	Number of chaetae				
				T. meridionalis	*T. kae*	*T. spectabilis* sp. nov.	*T. takensis* sp. nov.	*T. rungsimae* sp. nov.
Type-1	Ant. III	dorsal	latero-distal (AIIIO)	1	1	-	-	1
	Ant. III	ventral	latero-diatal (AIIIO)	-	-	1	1	-
	Ant.IVa	ventral	proximal	-	-	-	-	1
Type-2	Ant. I	ventral	basal	4	4	-	-	-
	Ant. II	dorsal	basal	2	2	2	1	2
	Ant. II	ventral	basal	-	-	1	1	1
Type-3	Ant. I	ventral	proximal	2	2	2	2	2
	Ant. II	ventral	proximal	1	1	-	1	1
	Ant. II	dorsal	proximal	-	-	1	-	-
Type-4	Ant.II	dorsal	AIIIO	-	-	-	-	2
	Ant.II	ventral	AIIIO	-	-	-	5	-
	Ant. III	dorsal	AIIIO	2	2	-	-	2
	Ant. III	ventral	AIIIO	-	-	2	2	-
	Ant.IVb	dorsal	lateral	-	-	-	-	1
	Ant.IVb	ventral	lateral	-	-	-	-	1
Type-5	Ant. I	ventral	all segment	7	6	-	8	-
	Ant. I	ventral	middle to proximal	-	-	2	-	3
	Ant. III	dorsal	AIIIO	2	2	-	-	2
	Ant. III	ventral	AIIIO	-	-	-	2	-
Type-6	Ant. I	dorsal	basal	3	3	3	2	3
	Ant. I	ventral	basal	-	-	3	3	3
Type-7	Ant. II	ventral	all segment	3	7	-	-	6
	Ant. III	dorsal	lateral	-	2	-	-	-
	Ant. III	ventral	middle to proximal	3	4	-	-	5
	Ant. IVa	dorsal	middle to proximal	4	4	-	-	-
	Ant. I	ventral	all segment	6	10	18	8	13
Type-8	Ant. II	dorsal	middle to proximal	9	8	5	8	13
	Ant. II	ventral	all segment	9	9	7	-	9
	Ant. II	ventral	proximal	-	-	-	8	-
	Ant. III	dorsal	all segment	10	15	-	14	20
	Ant. III	ventral	middle to proximal	11	6	6	-	11
	Ant. III	ventral	all segment	-	-	-	14	-
	Ant. IVa	dorsal	all segment	9	10	-	7	18
	Ant. IVa	ventral	all segment	13	5	2	12	20
	Ant. IVb	dorsal	all segment	9	9	23	-	18
	Ant. IVb	dorsal	basal	-	-	-	1	-
	Ant. IVb	ventral	all segment	11	-	4	8	15
	Ant. I	ventral	latero-proximal	2	1	5	1	1
Type-9	Ant. II	ventral	proximal	2	4	-	-	-
	Ant.IVa	ventral	latero-proximal	-	-	-	-	-
	Ant. I	ventral	latero-proximal	14	5	15	12	4
Type-10	Ant. II	ventral	proximal	2	5	-	-	-
	Ant. II	ventral	lateral	-	-	24	-	-
	Ant. II	ventral	latero-proximal	-	-	-	24	6
	Ant. III	dorsal	upper middle	-	1	14	-	-
	Ant. III	dorsal	all segment	-	-	-	9	-
	Ant. III	ventral	proximal	1	4	-	-	5
	Ant. III	ventral	all segment	-	-	34	23	-
	Ant. IVa	dorsal	middle to proximal	1	3	-	-	-
	Ant. IVa	dorsal	all segment	-	-	34	-	-
	Ant. IVa	ventral	all segment	-	-	60	8	12
	Ant. IVb	dorsal	middle	2	3	-	-	3
	Ant. IVb	dorsal	basal	-	-	3	-	7
	Ant. IVb	ventral	basal to middle	-	-	12	3	-
	Ant. IVa	dorsal	latero-proximal	-	1	-	-	-

Type of chaetae	Distribution on antenna	Location	Position on antennal segment	Number of chaetae				
				T. meridionalis	*T. kae*	*T. spectabilis* sp. nov.	*T. takensis* sp. nov.	*T. rungsimae* sp. nov.
Type-11	Ant. IVa	dorsal	all segment	-	-	10	10	22
	Ant. IVa	ventral	lateral	-	-	4	-	19
	Ant. IVb	dorsal	all segment	19	22	42	44	37
	Ant. IVb	ventral	all segment	35	36	40	18	45
	Ant. I	ventral	all segment	8	6	17	8	9
Type-12	Ant. I	ventral	lateral	-	-	-	3	-
Type-13	Ant. II	ventral	lateral	-	-	-	5	3
	Ant. III	ventral	lateral	-	-	-	3	-
	Ant. III	ventral	all segment	-	-	9	-	-
	Ant. IVa	dorsal	middle of Ant. IVa	-	3	-	-	-
	Ant. IVa	ventral	lateral	-	-	1	-	-
	Ant. IVa	ventral	middle	-	-	-	1	1
	Ant. II	dorsal	proximal	1	1	1	-	-
Type-14	Ant. III	dorsal	all segment	-	-	17	-	-
Type-15	Ant. III	ventral	middle to proximal	-	-	3	-	-
	Ant. III	ventral	all segment	-	-	-	13	-
	Ant. IVa	dorsal	all segment	-	-	10	-	-
	Ant. IVa	ventral	all segment	-	-	26	9	-
	Ant. IVb	ventral	all segment	-	-	22	6	-
Total of S-chaetae				208	207	485	308	347
Ordinary chaetae	Ant. I	dorsal	all segment	13	28	58	26	16
	Ant. I	ventral	all segment	27	38	113	58	
	Ant. II	dorsal	all segment	63	67	157	93	72
	Ant. II	ventral	all segment	68	77	161	69	63
	Ant. III	dorsal	all segment	45	38	167	97	64
	Ant. III	ventral	all segment	36	45	169	93	62
	Ant. IVa	dorsal	all segment	62	59	148	117	64
	Ant. IVa	ventral	all segment	53	60	142	98	58
	Ant. IVb	dorsal	all segment	49	48	150	65	138
	Ant. IVb	ventral	all segment	67	58	137	75	112
Total of ordinary chaetae				483	518	1,402	790	687
Total S-chaetae and ordinary chaetae				692	726	1,887	1,098	1,034
Subapical organ	Ant. IVb	dorsal	proximal near the tip	1	1	1	1	1
Scales	Ant. I	dorsal	all segment	19	25	127	58	29
	Ant. II	dorsal	basal to middle	25	13	152	13	30
	Ant. II	ventral	basal (to middle)	4	3	16	57	13
Overall antennal chaetae				741	768	2,183	1,228	1,107

these 5 species (see Tables 4 and 5). The new type of antenal chaetae discovered in this study (type 15) is found exclusively on the elongated antenna of *T. spectabilis* sp. nov. and *T. takensis* sp. nov. *Troglopedetes rungsimae* sp. nov., althought troglomorphic, has shorter antennae (873 μm) and, together with *T. meridionalis* and *T. kae*, does not present type 15 S-chaetae. This kind of chaetae was not detected in *Coecobrya sirindhornae* Jantarit, Satasook & Deharveng, 2019 and *Lepidonella doveri* (Carpenter, 1933), among the most troglomorphic Collembola regarding antennal elongation in Southeast Asia (Deharveng et al. 2018; Jantarit et al. 2019). In *Alloscopus* Börner, 1906, *Cyphoderus*, *Cyphoderopsis*, and *Rambusinella* Deharveng & Bedos, 1996 (Jantarit et al. 2013, 2014; Jantarit and Sangsiri 2020), we did not find this type 15 S-chaetae. Detailed analyses of antennal chaetae in other Entomobryoidea are lacking, and type 15 is so far a taxon-specific receptor limited to highly troglomorphic species of the genus *Troglopedetes*.

Table 5. Number of chaetae of each type along antennal segments in the three new species and in *T. meridionalis* and *T. kae*.

Type of S-chaetae/ antennal segment	*Troglopedetes meridionalis*						*Troglopedetes kae*						*Troglopedetes spectabilis* sp. nov.						*Troglopedetes takensis* sp. nov.						*Troglopedetes rungsimae* sp. nov.					
	Ant. I	Ant. II	Ant. III	Ant. IV		Total	Ant. I	Ant. II	Ant. III	Ant. IV		Total	Ant. I	Ant. II	Ant. III	Ant. IV		Total	Ant. I	Ant. II	Ant. III	Ant. IV		Total	Ant. I	Ant. II	Ant. III	Ant. IV		Total
				Ant. IVa	Ant. IVb					Ant. IVa	Ant. IVb					Ant. IVa	Ant. IVb					Ant. IVa	Ant. IVb					Ant. IVa	Ant. IVb	
Length (μm)	78	150	125	125	125	603	90	215	148	136	138	727	374	667	720	595	424	2,780	192	390	390	322	230	1,524	95	240	210	200	160	905
Type-1	-	-	1	-	-	**1**	-	-	1	-	-	**1**	-	-	1	-	-	**1**	-	-	1	-	-	**1**	-	-	1	1	-	**2**
Type-2	4	2	-	-	-	**6**	4	2	-	-	-	**6**	-	3	-	-	-	**3**	-	2	-	-	-	**2**	-	3	-	-	-	**2**
Type-3	2	1	-	-	-	**3**	2	1	-	-	-	**3**	2	1	-	-	-	**3**	2	1	-	-	-	**3**	2	1	-	-	-	**3**
Type-4	-	-	2	-	-	**2**	-	-	2	-	-	**2**	-	-	2	-	-	**2**	-	5	2	-	-	**7**	-	2	2	-	2	**6**
Type-5	7	-	2	-	-	**9**	6	-	2	-	-	**8**	2	-	-	-	-	**2**	8	-	2	-	-	**10**	3	-	2	-	-	**5**
Type-6	3	-	-	-	-	**3**	3	-	-	-	-	**3**	6	-	-	-	-	**6**	5	-	-	-	-	**5**	6	-	-	-	-	**6**
Type-7	-	3	3	4	-	**10**	-	7	6	4	-	**17**	-	-	-	-	-	**0**	-	-	-	-	-	**-**	-	6	5	-	-	**12**
Type-8	6	18	21	22	20	**87**	10	17	21	15	9	**72**	18	12	6	2	27	**65**	8	16	28	19	9	**80**	13	22	31	38	33	**137**
Type-9	2	2	-	-	-	**4**	1	4	-	-	-	**5**	5	-	-	-	-	**5**	1	-	-	-	-	**1**	1	-	-	-	-	**1**
Type-10	14	2	1	1	2	**20**	5	5	5	3	3	**21**	15	24	48	94	15	**196**	12	24	32	8	3	**79**	4	6	5	12	10	**36**
Type-11	-	-	-	-	54	**54**	-	-	-	1	58	**59**	-	-	-	14	82	**96**	-	-	-	10	62	**72**	-	-	-	41	82	**123**
Type-12	8	-	-	-	-	**8**	6	-	-	-	-	**6**	17	-	-	-	-	**17**	8	-	-	-	-	**8**	9	-	-	-	-	**9**
Type-13	-	-	-	-	-	**0**	-	-	-	3	-	**3**	-	-	9	1	-	**10**	3	5	3	1	-	**12**	-	3	-	1	-	**4**
Type-14	-	1	-	-	-	**1**	-	1	-	-	-	**1**	-	1	-	-	-	**1**	-	-	-	-	-	**0**	-	-	-	-	-	**0**
Type-15	-	-	-	-	-	**0**	-	-	-	-	-	**0**	-	-	20	36	22	**78**	-	-	13	9	6	**28**	-	-	-	-	-	**-**
Overall S-chaetae	46	29	30	27	76	**208**	37	37	37	26	70	**207**	65	41	86	147	146	**485**	48	53	81	47	80	**308**	38	43	46	93	127	**347**
Overall ordinary chaetae	40	131	81	115	116	**483**	66	144	83	119	106	**518**	171	318	336	290	287	**1402**	84	162	190	214	140	**790**	54	135	126	122	250	**687**
Total S- and ordinary chaetae	86	160	111	142	193	**692**	103	181	119	145	177	**726**	236	359	422	437	433	**1887**	132	215	271	261	220	**1099**	92	178	172	215	377	**1034**
Subapical organite	-	-	-	-	1	**1**	-	-	-	-	1	**1**	-	-	-	-	1	**1**	-	-	-	-	1	**1**	-	-	-	-	1	**1**
Scale	19	29	-	-	-	**48**	25	16	-	-	-	**41**	127	168	-	-	-	**295**	58	70	-	-	-	**128**	29	43	-	-	-	**72**
Overall chaetae	105	189	111	142	194	**741**	128	197	119	145	178	**768**	363	527	422	437	434	**2183**	189	285	271	262	221	**1228**	121	221	172	215	378	**1107**

It seems that antennal phanerotaxy in the genus *Troglopedetes* is richer than in other Entomobryidae described so far. For example, 13 types of chaetae are reported in *Alloscopus* (Jantarit and Sangsiri 2020) and *Cyphoderopsis* (Jantarit et al. 2013), 12 types in *Verhoeffiella* (Lukić et al. 2015, 2018), at least 10 types in *Lepidonella* (Deharveng et al. 2018), and at least 12 types in *Rambutsinella* (unpublished data).

Generally, the length of antennal segments in Thai *Troglopedetes* ranked as Ant. IV (a+b) > II > III > I (Deharveng 1988a, 1990; Deharveng and Gers 1993; Jantarit et al. 2020), including *T. multispinosus*, which is second for antennal elongation in the genus in Thailand (ratio of antennae: body = 0.9). However, in the most troglomorphic species of the genus, *T. spectabilis* sp. nov., antennal segment length ranked as Ant. IV (a+b) > III > II > I. In *T. takensis* sp. nov. the length of Ant. II and III is a similar value and ranked as IV (a+b) > (II = III) > I. while *T. rungsimae* sp. nov. antennal segment length ranked as Ant. IV (a+b) > II > III > I. Hence, antennal length, which is a troglomorphic character, is not the result of a similar proportional increase of all antennal segments, as already observed in other cave species groups like *Verhoeffiella* (see Lukic et al. 2018).

According to the study of Jantarit et al. (2020), the number of chaetae parallels the length of antennal segments only for the overall result and for ordinary chaetae, but not for S-chaetae. A similar conclusion can be drawn from this study (Tables 5 and 6). Ant. IV (a+b), the longest segment, carries less S-chaetae types (only 5–6 types) than other segments (Table 5). The distal subsegment of Ant. IV (Ant. IVb) has more kinds and a higher density of S-chaetae than the proximal one (Ant. IVa), although their relative length is subequal to equal (Jantarit et al. 2020). In this study, all three new species have Ant. IVa 1.25–1.4 times longer than Ant. IVb (Tables 1–3). However, in *T. spectabilis* sp. nov., Ant. IVa and Ant. IVb possesses a similar number of S- and ordinary chaetae, but *T. takensis* sp. nov. and *T. rungsimae* sp. nov. have more S-chaetae in Ant. IVb than Ant. IVa (Table 5). Type 10 and type 11 S-chaetae have a more complex arrangement and are more numerous in Ant. IV (a+b) than other segments. The number of type 10 S-chaeatae is higher in Ant. IVa ventrally, while type-11 is instead widespread in both dorsal and ventral sides of Ant. IVb in all described species (Table 5). Ordinary chaetae are normally more numerous in Ant. IVa than Ant. IVb because it is relatively longer than Ant. IVb, except in *T. rungsimae* sp. nov. where ordinary chaetae in Ant. IVb are significantly higher in number than Ant. IVa.

Table 6. Number of subcylindrical type 10 S-chaetae on antennal segments I, II and III ventrally in the three new species from Thailand and three Mediterranean cave species.

Species/Antennal segment	Ant. I	Ant. II	Ant. III	Country	Source
T. absoloni	3–5	15	15	Spain	Soto-Adames et al. 2014
T. ildumensis	2–5	25–30	25–30	Spain	Soto-Adames et al. 2014
T. kae	5	5	5	Thailand	Jantarit et al. 2020
T. meridionalis	14	2	1	Thailand	Jantarit et al. 2020
T. ruffoi	9	31	34	Italy	Fanciulli et al. 2003
T. rungsimae sp. nov.	4	6	5	Thailand	This study
T. spectabilis sp. nov.	15	24	48	Thailand	This study
T. takensis sp. nov.	12	24	32	Thailand	This study

On Ant. I, the shortest segment, the number of S-chaetae varies depending on species. In *T. meridionalis* and *T. kae*, Ant. I has more S-chaetae than Ant. II and III, while in *T. spectabilis* sp. nov., Ant. I has more S-chaetae than Ant. II only (Table 5). Conversely, *T. takensis* sp. nov. and *T. rungsimae* sp. nov. have less S-chaetae on Ant. I than on Ant. II and III. However, in all the described species, Ant.I is clearly richer than other segments in diversity of S-chaetae, with 7–8 S-chaetal types, emphasizing the importance for sensorial functions in this segment (Jantarit et al. 2020).

Ant. II is the second longest segment for the moderate long antennal species (*T. rungsimae* sp. nov. and also in *T. meridionalis* and *T. kae*), but it can be shorter than (*T. spectabilis* sp. nov.) or subequal to (*T. takensis* sp. nov.) Ant. III for the species with very long antennae. This segment has less S-chaetae than Ant. III (Table 5).

Ant. III is the second longest segment in species with very long antennae (*T. spectabilis* sp. nov., and *T. takensis* sp. nov.) and carries the highest number of S-chaetae after Ant. IV (Table 5). However, this segment ranks third in length for the moderately long-antenna species (*T. rungsimae* sp. nov., *T. meridionalis* and *T. kae*) and has a number of S-chaetae similar to Ant. II. Special to this segment is a group of S-chaetae of type 10 located latero-ventrally in the highly troglomorphic species (discussed below) and at the level of the antenna III organ (AIIIO). The AIIIO of the described species has at least 5 S-chaetae (one chaeta of type 1, two chaetae of type 4 and two chaetae of type 5, Figs 6C, D, 11C, 12D), like in *T. kae* and *T. meridionalis*. Two chaetae of type 4 are obviously sprinkled with pores. The AIIIO of Thai *Troglopedetes* is normally located apically in the latero-dorsal side of the antennae, except in *T. spectabilis* sp. nov. and *T. takensis* sp. nov. where it is obviously on the ventral side of the segment.

Meanwhile, the ventral side of the antennal segment possesses a higher number of chaetae than the dorsal one both in overall chaetae and S-chaetae (Table 4, Figs 5–7, 11–13). This is probably because the targets of the sensorial receptors are more commonly found at ground level than above. Collembola antennae are also often raised and waved in the air (pers. observation), probably to pick up stimuli from objects and thus sensorial receptors on the ventral side may be more effective at detecting.

The diversity of antennal chaetae in Thai *Troglopedetes* does not differ significantly between the extremely long antennae and the moderately long antennae species. *T. spectabilis* sp. nov., the longest antennae species so far, has 21 types of chaetae (5 types of ordinary chaetae, 14 type of S-chaetae, a subapical organite and scale), whereas *T. takensis* sp. nov., *T. rungsimae* sp. nov. (long antennae) and *T. kae* (moderate long antennae) all have 20 types of chaetae (5 types of ordinary chaetae, 13 S-chaetal types, subapical organite and scale). *Troglopedetes meridionalis* (moderate long antennae) has 19 types of chaetae (5 types of ordinary chaetae, 12 S-chaetal types, subapical organite and scale) (Tables 4 and 5). It has long been known that antennal chaetae are associated with sensorial reception and cave adapted species are expected to sustain more numerous, larger or more diverse chaetae than surface species (Deharveng 1988b; Thibaud and Deharveng 1994; Lukić 2019). No increase in size or morphological diversity of chaetae has been observed in our species from more to less troglomorphic species. The only increase in sensorial potential is linked to the increase of chaetae number linked to the increase in size of antennae. However, the numerous non-cave

species of the genus in Southeast Asia are still undescribed and have not been examined in this respect. More thorough studies therefore need to be done before drawing any conclusion, i.e. habitat preferences (cave vs. surface species), cave adaptation (troglomorphy vs. non-troglomorphy), sex (male vs. female) or life cycle (juvenile vs. adult). In any case, *Troglopedetes* is a good model to develop such investigations because of its large range of life styles (soil litter to cave) and morphological adaptations to the subterranean life.

Groups of subcylindrical S-chaetae (type 10) on antennal segments I, II and III deserve to be mentioned here. There are clusters of numerous S-chaetae in three Mediterranean cave species (*T. ruffoi*, *T. absoloni* and *T. ildumensis*) (Fanciulli et al. 2003; Soto-Adames et al. 2014; Table 6). This type of chaetae was detected in all the described *Troglopedetes* of Thailand and observed in several other undescribed species from soil and caves in the country. Among them all non troglomorphic species bear a small number of S-chaetae type 10 (<6) that are not grouped in clusters, but the two new elongated antennae species (*T. spectabilis* sp. nov. and *T. takensis* sp. nov.) show this cluster of S-chaetae type 10 on the ventral side of antennal segments I, II and III, constituting a large number of such chaetae than some of the Mediterranean species (Figs 5B, 6B, 6D, 11B, 12B, 12D, Tables 4–6). At this point, cluster of a high number of type 10 chaetae appears as a troglomorphic character in *Troglopedetes* species.

Although the function of individual chaetal types of Collembola antennae is little known, differences in the morphological structure of chaetae are likely to enable springtails to receive a wide range of different stimuli, responding to light, smell, taste, sound, touch, vibration, stretch, temperature, humidity, a multitude of chemical agents and concentration gradients of oxygen and carbon dioxide (Altner and Prillinger 1980; Hartenstein 1997; Hopkin 1997). We are convinced that the study of antennal chaetae in Collembola not only has important value for taxonomy, but would also bring a significant contribution in several areas for morphologists, physiologists and developmental biologists. From this perspective, ultrastructural data as a first insight into their functions are dramatically lacking.

Key to Thai species of *Troglopedetes*

1 Central area of head macrochaetae absent **2**
– Central area of head macrochaetae present **3**
2 Eyes absent but each ocular area with 2 black spots; claw without inner teeth; tenent hair pointed; antenna as long as the body ..... ***T. takensis* sp. nov.**
– Eyes and ocular patches absent; claw with 2 inner teeth; tenent hair clavate; antenna 0.6 times shorter than the body ..... ***T. calvus* Deharveng & Gers, 1993**
3 Central area of head with 1–2+1–2 macrochaeta(e) (A and E mac) **4**
– Central area of head with 3+3 macrochaetae (A, B or C, and E mac) **6**
– Central area of head with 4–6+4–6 macrochaetae (A, B, E (C, D, F, G) mac) **8**
– Central area of head with 7+7 macrochaetae (A–G mac) **13**

4 Central area of head with 1+1 macrochaetae (A mac); lateral flap of ventral tube with 6 chaetae; tenent hair pointed; internal row of dens with 30–37 spines..... ***T. meridionalis*** **Jantarit, Surakhamhaeng & Deharveng, 2020**

– Central area of head with 1–2+1–2 macrochaetae (A and E mac); lateral flap of ventral tube with 7 chaetae; tenent hair clavate; internal row of dens with 18–24 spines..... **5**

5 Abd. IV with 2+2 central mac; claw with 2 inner teeth ..... ***T. paucisetosus*** **Deharveng & Gers, 1993**

– Abd. IV with 3+3 central mac; claw with 1 inner tooth ..... ***T. convergens*** **Deharveng & Gers, 1993**

6 Head macrochaetae with A, B, E mac; body length 1.8–2.2 mm; internal row of dens with 34–41 spines..... ***T. multispinosus*** **Deharveng & Gers, 1993**

– Head macrochaetae with A, C, E mac; body length 0.9–1.4 mm; internal row of dens with 25–29 spines..... **7**

7 Antenna as long as the body; body length 0.9–1.0 mm; lateral flap of ventral tube with 8 chaetae..... ***T. rungsimae*** **sp. nov.**

– Antenna 0.6 times shorter than the body; body length 1.3–1.4 mm; lateral flap of ventral tube with 7 chaetae..... ***T. dispersus*** **Deharveng & Gers, 1993**

8 1–2+1–2 eyes; outer maxillary lobe with 1 sublobal hair..... ***T. microps*** **Deharveng & Gers, 1993**

– Eyes absent; outer maxillary lobe with 2 sublobal hair; Abd. IV with 3+3 central mac **9**

9 Th. II with 9+9 central mac; labial formula: M1m2rel1l2; antenna very long about 1.8 times longer than the body..... ***T. spectabilis*** **sp. nov.**

– Th. II with 8+8 central mac; inter teeth of claw with 1+1 ..... **10**

10 Head macrochaeta D present; labial formula: M1M2ReL1l2; antenna 0.8 times shorter than the body ..... ***T. longicornis*** **Deharveng & Gers, 1993**

– Head macrochaeta D absent; labial formula: M1M2REL1l2; antenna 0.4–0.5 times shorter than the body **11**

11 Central area of head with 5+5 macrochaetae; Th. II with 8+8 central mac, Abd.IV with 3+3 central mac; dens 15 times longer than the mucro..... ***T. fredstonei*** **Deharveng, 1988**

– Central area of head with 4+4 macrochaetae; Th. II with 8+8 central mac, Abd. IV with 3+3 central mac; dens 8.8–14 times longer than the mucro..... **12**

12 Lateral flap with 6+6 chaetae; internal row of dens with 26–33 spines; mucro with 5 teeth ..... ***T. kae*** **Jantarit, Surakhamhaeng & Deharveng, 2020**

– Lateral flap with 7+7 chaetae; internal row of dens with 37–42 spines; mucro with 4 teeth ..... ***T. centralis*** **Deharveng & Gers, 1993**

13 Eyes absent, outer maxillary lobe with 1 sublobal hair; Th. II with 9+9 central mac; Abd.IV with 3+3 central mac **14**

– 3+3 eyes, outer maxillary lobe with 2 sublobal hairs; Th. II with 8+8 central mac; Abd. IV with 2+2 central mac ..... ***T. leclerci*** **Deharveng, 1990**

14 Labial formula: M1M2REL1l2; body length 1.1–1.2 mm ..... ***T. maungonensis*** **Deharveng & Gers, 1993**

– Labial formula: M1M2ReL1l2; body length 1.3–1.75 mm ..... ***T. maffrei*** **Deharveng & Gers, 1993**

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References

Altner H, Prillinger L (1980) Ultrastructure of invertebrate chemo-, thermo- and hygroreceptors and its functional significance. International Review 67: 69–139. https://doi.org/10.1016/S0074-7696(08)62427-4

Besson J-P, Deharveng L, Bréhier F (2001) Laos. In: Juberthie C, Decu V (Eds) Encyclopædia Biospeologica, tome III. Société de Biospéologie, Moulis, France, 1883–1889.

Börner C (1906) Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums., Mitteilungen aus den Naturhistorischen Museum in Hamburg, XXIII. Jahrgang, 2. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Austalten. XXIII. 1905., Hamburg, 1906, 147–188.

Carpenter GH (1917) Zoological results of the Abor Expedition 1911–12: Collembola. Records of the Indian Museum, Calcutta 8: 561–568. https://doi.org/10.5962/bhl.part.1186

Christiansen K (2012) Morphological adaptations. In: Culver DC, White WB (Eds) Encyclopedia of Caves, 2nd edn. Academic Press, Elsevier, 517–528. https://doi.org/10.1016/B978-0-12-383832-2.00075-X

Deharveng L (1981) La chétotaxie dorsale de l'antenne et son intérêt phylogénétique chez les Collemboles Neanuridae. Nouvelle Revue d'Entomologie 11(1): 3–13.

Deharveng L (1983) Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée Neanurienne. Travaux du Laboratoire d'Ecobiologie des Arthropodes Edaphiques, Toulouse 4: 1–63.

Deharveng L (1987) Cave Collembola of South-East Asia. The Korean Journal of Systematic Zoology 3: 165–174.

Deharveng L (1988a) A new troglomorphic Collembola from Thailand: *Troglopedetes fredstonei*, new species (Collembolan: Paronellidae). Bishop Museum Occasional Papers 28: 95–98.

Deharveng L (1988b) Collemboles cavernicoles VII- *Pseudosinella bessoni* n. sp. et note sur l'évolution morphologique de la griffe chez les *Pseudosinella*. Revue Suisse de Zoologie 95(1): 203–208. https://doi.org/10.5962/bhl.part.79648

Deharveng L (1990) Fauna of Thai caves II. New Entomobryoidea Collembola from Chiang Dao cave, Thailand. Bishop Museum Occasional Papers 30: 279–285.

Deharveng L, Bedos A (1995) *Lepidonella lecongkieti* n. sp., premier Collembole cavernicole du Vietnam (Collembola, Paronellidae). Bulletin de la Société entomologique de France 100(1): 21–24. https://doi.org/10.3406/bsef.1995.17118

Deharveng L, Bedos A (1996) *Rambutsinella*, a new genus of Entomobryidae (Insecta: Collembola) from southeast Asia. Raffles Bulletin of Zoology 44(1): 279–285.

Deharveng L, Bedos A (2018) Diversity of terrestrial invertebrates in subterranean habitats. In: Moldovan OT, Kovác L, Halse S (Eds) Cave Ecology, Ecological Studies 235. Springer Nature, Cham, 107–172. https://doi.org/10.1007/978-3-319-98852-8_7

Deharveng L, Gers C (1993) Ten new species of *Troglopedetes* Absolon, 1907 from caves of Thailand (Collembola, Paronellidae). Bijdragen tot de Dierkunde 63: 103–113. https://doi.org/10.1163/26660644-06302002

Deharveng L, Kiet LC, Bedos, A (2001) Vietnam. In: Juberthie C, Decu V (Eds) Encyclopaedia Biospeologica, tome II. Société de Biospéologie, Moulis, 2027–2037.

Deharveng L, Jantarit S, Bedos A (2018) Revisiting *Lepidonella* Yosii (Collembola: Paronellidae): character overview, checklist of world species and reassessment of *Pseudoparonella doveri* Carpenter. Annales de la Société entomologique de France (N.S.), 54(5): 381–400. https://doi.org/10.1080/00379271.2018.1507687

Fanciulli PP, Inguscio S, Rossi E, Dallai R (2003) Nuovi ritrovamenti di *Troglopedetes ruffoi* Delamare Deboutteville (Collembola, Paronellidae). Thalassia Salentina 26: 201–206.

Fjellberg A (1999) The labial palp in Collembola. Zoologischer Anzeiger 237: 309–330.

Gisin H (1967) Espèces nouvelles et lignées évolutives de *Pseudosinella* endogées (Collembola). Memorias e Estudos do Museu Zoologico da Universidade de Coimbra 30: 1–21.

Hartenstein V (1997) Introduction to insect sensory organs as a model system in sensory physiology and developmental biology. Microscopy Research and Technique 39: 467–469. https://doi.org/10.1002/(SICI)1097-0029(19971215)39:6%3C467::AID-JEMT1%3E3.0.CO;2-B

Hopkin SP (1997) Biology of the springtails (Insecta: Collembola). Oxford University Press, 340 pp.

Jantarit S, Sangsiri T (2020) Two new species of *Alloscopus* from caves in Thailand, with a key to world species of the genus (Hexapoda: Collembola). Raffles Bulletin of Zoology 35: 48–60. http://dx.doi.org/10.26107/RBZ-2020-0037

Jantarit S, Bedos A, Deharveng L (2016) An annotated checklist of the collembolan fauna of Thailand. Zootaxa 4169(2): 301–360. https://doi.org/10.11646/zootaxa.4169.2.4

Jantarit S, Satasook C, Deharveng L (2013) The genus *Cyphoderopsis* (Collembola: Paronellidae) in Thailand and a faunal transition at the Isthmus of Kra in Troglopedetinae. Zootaxa 3721(1): 49–70. https://doi.org/10.11646/zootaxa.3721.1.2

Jantarit S, Satasook C, Deharveng L (2014) Cyphoderus (Cyphoderidae) as a major component of collembolan cave fauna in Thailand, with description of two new species. ZooKeys 368: 1–21. https://doi.org/10.3897/zookeys.368.6393

Jantarit S, Satasook C, Deharveng L (2019) *Coecobrya sirindhornae* sp. nov., the most highly troglomorphic Collembola in Southeast Asia (Collembola, Entomobryidae). ZooKeys 824: 21–44. https://doi.org/10.3897/zookeys.824.31635

Jantarit S, Surakhamhaeng K, Deharveng L (2020) The multiformity of antennal chaetae in *Troglopedetes* Joseph, 1872 (Collembola, Paronellidae, Troglopedetinae), with descriptions of two new species from Thailand. Zookeys 987: 1–40. https://doi.org/10.3897/zookeys.987.54234

Jordana R, Baquero E (2005) A proposal of characters for taxonomic identification of *Entomobrya* species (Collembola, Entomobryomorpha) with description of a new species. Abhandlungen und Berichte Naturkundemuseums Goerlitz 76: 117–134.

Joseph G (1872) Beobachtungen über die Lebensweise und Vorkommen den in den Krainer Gebirgsgrotten einheimischen Arten der blinden Gattungen *Machaerites*, *Leptodirus*, *Oryotus* und *Troglorrhynchus*. Jahres-Bericht der Schlesischen Gesellschaft für Vaterländische Cultur 49: 171–182.

Lukić M (2019) Collembola. In: White WB, Culver DC, Pipan T (Eds) Encyclopedia of Caves, thrid edition. Academic Press, Elsevier, 308–318. https://doi.org/10.1016/B978-0-12-814124-3.00034-0

Lukić M, Porco D, Bedos A, Deharveng L (2015) The puzzling distribution of *Heteromurus* (*Verhoeffiella*) *absoloni* Kseneman, 1938 (Collembola: Entomobryidae: Heteromurinae) resolved: detailed redescription of the nominal species and description of a new species from Catalonia (Spain). Zootaxa 4039(2): 249–275. https://doi.org/10.11646/zootaxa.4039.2.3

Lukić M, Delić T, Zagmajster M, Deharveng L (2018) Setting a morphological framework for the genus *Verhoeffiella* (Collembola, Entomobryidae) for describing new troglomorphic species from the Dinaric karst (Western Balkans). Invertebrate Systematics 32: 1118–1170. https://doi.org/10.1071/IS17088

Mitra SK (1993) Chaetotaxy, phylogeny and biogeography of Paronellinae (Collembola: Entomobryidae). Records of the Zoological survey of India, Occasional Paper 154: 1–100.

Schäffer C (1897) Apterygoten. Hamburger Magalhaensische Sammelreise Apterygoten 8: 1–48.

Soto-Adames FN, Jordana R, Baquero E (2014) Comparative analysis of the dorsal chaetotaxy of *Troglopedetes*, *Trogolaphysa*, and *Campylothorax* supports the synonymization of tribes Paronellini and Troglopedetini (Collembola: Paronellidae). Journal of Insect Science 14(1): 1–16. https://doi.org/10.1093/jisesa/ieu140

Soto-Adames FN (2015) The dorsal chaetotaxy of first instar *Trogolaphysa jataca*, with description of twelve new species of Neotropical *Trogolaphysa* (Hexapoda: Collembola: Paronellidae). Zootaxa 4032(1): 1–41. https://doi.org/10.11646/zootaxa.4032.1.1

Szeptycki A (1979) Chaetotaxy of the Entomobryidae and its phylogenetical significance. Morpho-systematic studies on Collembola. IV. Polska Akademia Nauk, Zakład Zoologii Systematycznej i Doświadczalnej, Państwowe Wydawnictwo Naukowe, Warszawa-Kraków, 219 pp.

Thibaud JM, Deharveng L (1994) Collembola. In: Juberthie C, Decu V (Eds) Encyclopaedia Biospeologica, tome I. Société de Biospéologie, Moulis, 267–276.

Yosii R (1956) Höhlencollembolen Japans II. Japanese Journal of Zoology 11: 609–627.

Yosii R (1960) On some Collembola of New Caledonia, New Britain and Solomon Islands. Bulletin of the Osaka Museum of Natural History 12: 9–38.

Zhang F, Deharveng L (2014) Systematic revision of Entomobryidae (Collembola) by integrating molecular and new morphological evidence. Zoologica Scripta 44(3): 298–311. https://doi.org/10.1111/zsc.12100